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VOLUME 63

# PHYLETIC ANALYSIS OF FIFTY CHARACTERS OF ADVANCED SNAKES

HYMEN MARX

*and*

GEORGE B. RABB

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VOLUME 63

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CHICAGO, U. S. A.

# PHYLETIC ANALYSIS OF FIFTY CHARACTERS OF ADVANCED SNAKES

**FIELDIANA**
**Zoology**

**Published by Field Museum of Natural History**

VOLUME 63

# PHYLETIC ANALYSIS OF FIFTY CHARACTERS OF ADVANCED SNAKES

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# INTRODUCTION

There has been a long standing dichotomy of views concerning the phylogenetic relationships of the venomous snakes. One view has considered the families of hollow-fanged snakes as a single derivation from the "non-venomous" colubrid snakes, which group contains the vast majority of extant snakes. Opposing stands have been taken by many other authors who have argued for separate origins of the vipers and the proteroglyphous elapids and hydrophiids.

In recent years the picture has become more complicated as major taxonomic rearrangements of the advanced snakes have been proposed (Underwood, 1967) and new allocations have been made of problematic venomous taxa (Bourgeois, 1965; MacDowell, 1968; Kochva and Wolberg, 1970). In pursuit of a better understanding of the evolutionary development of the venomous snakes, we have undertaken a broad survey of characteristics of the advanced snakes, the Colubroidea. The aim has been to identify the course of evolution of the groups now known as the Viperidae, Elapidae, and Hydrophiidae by close analysis of the distribution of variation among taxa within these groups, using the Colubridae as our reference standard.

This text is essentially a catalogue of our findings on the phyletics of 50 characters. Major discussions and syntheses of the findings remain for the future. Our approach to the phyletics of characters has been set forth earlier (Marx and Rabb, 1970) and what follows here is based on that account. In general, in phyletic character studies one must (1) select characters for analysis, (2) differentiate character states, (3) determine derivativeness of states of characters, (4) deduce directions of change in multiple state characters.

## SELECTION OF CHARACTERS

Ultimate application of the study in helping determine the evolutionary paths among and within the venomous taxa influenced us to analyze many characteristics considered distinctive of these groups. We were interested, too, in trying our pragmatic methodology on various kinds of characters. One breakdown of the 50 characters in this text shows 35 to be qualitative, 8 meristic, and 7 mensurative. About half are skeletal features and half are integumentary. Among others, we included trivial features (serration of scales), traditional data (number of scale rows), common but perplexing characteristics (presence or absence of apical scale pits), and proportional measurements (relative length of dentary). A preponderance of the 50 characters are cephalic. We have justified this by reference to Gans (1962), who makes a strong argument for this region being the major active site of evolutionary change in snakes.

The data came from three principal sources: Boulenger's Catalogues (1893–96), a suite of references on snakes of various regions (see Marx and Rabb, 1970), and a working sample of about 1,000 skulls representing 510 species (see pp. 305–310). In tables and text, we have segregated data on *Azemiops* and *Atractaspis,* venomous genera of particular interest because of their uncertain relationships to the vipers.

It is obvious in numerous cases that the sample was too small for statistical testing. Where useful, chi-square tests were applied to the data; "significantly" refers to a probability level of .05 or better.

## DIFFERENTIATION OF CHARACTER STATES

Morphological characters are ordinarily defined in terms of more or less discrete anatomical features or units. More importantly, characters in taxonomic use are relative and must be defined in terms of some variation—a smooth surface in an organism is not significant if there is no rough surface in some related form. Characters may also be relative in regard to the units or classes included. Usually, the units of a character represent variations of the same topographic structure or are serial homologues. However, the classes may be comprised of relationships among structures and here the limits of a character can be chosen to fit the analytic goal. Examples in this text include characters 10 and 12, where 10 is a further specification of structural relationships covered more grossly in 12. Character states, often equivalent to classes in qualitative characters, are major indices of variation of a character. In establishing classes and states in this study, our concerns were two: that a character class or state existed in an evolutionarily meaningful way, and that the frequency of its existence would be used in analyzing the phyletics of the character (i.e., its evolutionary course). To these ends we related characters to intraspecific and interspecific variation, thus using species in two ways as genetic measures.

Intraspecific variation has been recognized in quantitative characters in terms of a span, or minimal non-ordinal range, common to the vast majority of species. This measure was used to segment the entire range of variation into classes. In fitting the species to these classes, their variation was minimized by using the arithmetic means of individual specimen values in the case of most quantitative characters (ranges in four instances—see Character 11). For the more qualitative characters, individual specimens were assigned to classes formed about visual modal points. In these cases, and where the classes were of a sharply defined, presence or absence nature, some species had a range over more than one class.

In defining character states by using variation among species, we inspected the class frequency distributions of species in familial groupings (for example see Table 6). The extremes of the character marked by major breaks in the distribution were denoted as separate states. In many of the quantitative characters numerous classes were thus lumped into a few states. In qualitative characters with exclusive classes, we generally recognized a state containing species that fell in more than one class. With few states in a character there are large enough sample sizes to give some confidence to the relative frequency and correlations approach to phyletic analysis. For two characters not included here, shapes of the ectopterygoid and premaxilla, the numerous classes were not reducible to a few states.

Since generic units at the least summarize interspecific variation, data are included in this form in the tables and text, but the analyses are ordinarily based on the frequency distributions of the species. Originally, we were concerned with segmenting the data so that most genera in the Viperidae would be segregated in multistate characters, but this proved impractical.

# CRITERIA FOR DERIVATIVENESS OF CHARACTER STATES

Ten criteria for designating character states as derived or primitive are given below, followed in parentheses by the number of applications in this study (in states, characters).

1. Uniqueness. A character state is derived if that state is unique to a "descendent" group. (16, 13)
2. Relative abundance. A character state widely distributed in the ancestral group is primitive for descendent groups because such a state has a greater probability of having had its genotype transferred to various descendent stocks than does a rare state. (80, 41)
3. Correlation of derived states. A character state is derived if its occurrence is positively correlated with derived states of other characters. Such correlation of derived states of different characters probably results from common genetic history of taxa. (72, 40)
4. Morphological specialization. A character state is derived if it is predominant in some adaptive specialization. Within a given stock several morphological structures may be used to accomplish the same function. Within a homogeneous group a specialized function is usually accomplished with the same structure. (12, 9)
5. Ecological specialization. A character state is derived when it is relatively more abundant in taxa with a particular mode of life. (72, 43)
6. Geographic restriction. A character state is derived if it is predominant in taxa from a particular geographic area. In accord with the low vagility of snakes, a characteristic so limited implies a closer historical (phylogenetic) relationship for taxa having this characteristic than for neighboring taxa not phenetically similar or taxa from different geographic areas. (18, 14)
7. Closely related taxa. A character state is derived if it is chiefly abundant in a restricted morphologically homogeneous group

of taxa since that state probably has a common origin in these taxa. (11, 9)

8. Correlation of applied criteria. A character state is considered more probably derived if two or more of the above criteria agree in indicating phyletic direction. Therefore, the more criteria applicable to a character's states, the greater confidence attaches to interpretation of direction. (79, 45)
9. Genetic structure. For characters usually employed in taxonomic studies of snakes, there is practically no information on the genetic bases of variation or on the effects of developmental and environmental influences on genetically based variation. (0)
10. Fossil record. Again, knowledge is so fragmentary in regard to fossils of advanced snakes that we have been unable to apply data from this source. (0)

In this study, the heterogeneous, widespread, and abundant family Colubridae was designated as phenetically representing the ancestral group (Marx and Rabb, 1970, p. 530). This is equivalent to "out-group" comparative analysis (Throckmorton, 1968).

## DIRECTIONAL SEQUENCE CRITERIA

When only two states occur in a character, all that is required for designation of directional sequence is to determine which state is derived. However, criteria can also be applied to determine directional relations of character states when three or more states occur. Sequences are either in a single direction, or in different directions. Combinations of directional change may occur when there are four or more character states.

Directional sequence cannot be determined when one state is a necessary correlate of another state. We have not refined our analysis to consider correlations of states of one character with different derived states of another character. Cursory inspection shows that such an approach would be fruitful.

Indicative of different directions in sequences of states of a particular character are:

1. derived states correlate mostly with derived states of different other characters
2. taxa in the derived states are predominantly abundant in different habitat zones
3. derived states perform different functions
4. the primitive state has a logically intermediate relation to other states
5. derived states are overwhelmingly abundant in different unrelated taxa
6. derived states are abundant in taxa from different major geographic areas

Criteria indicating a single directional sequence of different states of a particular character are:

1. a derived state represents intraspecific (or intrageneric) variation between two other states
2. derived states are correlated mostly with derived states of the same characters

3. taxa in the different states are predominantly abundant in the same habitat zones
4. the states perform the same function
5. a derived state is a logically intermediate condition between other states in a single gradient morphological continuum

To determine the sequential order of derived states in a single direction, we depended on variational intermediacy (Criteria 1 and 5, immediately above) and relative derivativeness of states (from Criteria 1, 2, 3, 5, 6, and 8 of preceding section).

## TYPES OF CHARACTER STATE TREES

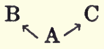
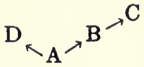
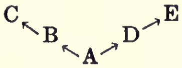
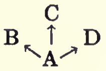
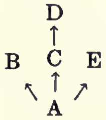
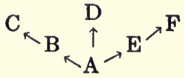
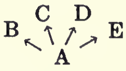
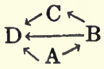
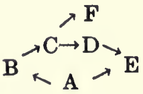
Commonly, results of phyletic analysis are presented in the form of character state trees. These are of three basic patterns: unidirectional, characters evolve their states in a single direction; multidirectional, characters evolve their states in two or more directions; circular, characters evolve their states in one or more directions, but have some convergence to a single character state. Combinations of these various types of trees occur in this survey (see below).

The analysis of the 50 characters produced 12 types of these basic three patterns. The maximum number of states for a single character is 6, with a mean of 3.38 states per character. There is a total of 169 states, 50 primitive and 119 derived.

Two additional kinds of characters also occur in a survey of this nature: single state and nondirectional characters. Single state characters are not susceptible to phyletic analysis within the group (e.g., no eyelids in snakes). Nondirectional characters are those characters with more than one state and their direction cannot be determined. This may occur when two or more states have no criteria applicable to them, or when a necessary correlate occurs between two or more states (see Character 30).

The types of character trees encountered in this study are given on page 10.

## TYPES OF EVOLUTIONARY CHARACTER PATHS

| Number of states | Number of characters | Character Tree | Characters |
|---|---|---|---|
| | | UNIDIRECTIONAL | |
| 2 | 7 | A→B | 4 6 14 15 18 34 35 |
| 3 | 15 | A→B→C | 3 8 10 12 17 19 21 23 24 27 30 32 36 43 48 |
| 4 | 2 | A→B→C→D | 2 45 |
| | | MULTIDIRECTIONAL<br>Bidirectional | |
| 3 | 9 |  | 7 9 25 38 39 42 44 49 50 |
| 4 | 9 |  | 11 13 16 20 22 26 28 37 41 |
| 5 | 1 |  | 1 |
| | | Tridirectional | |
| 4 | 2 |  | 31 46 |
| 5 | 1 |  | 33 |
| 6 | 1 |  | 47 |
| | | Quadridirectional | |
| 5 | 1 |  | 5 |
| | | CIRCULAR | |
| 4 | 1 |  | 29 |
| 6 | 1 |  | 40 |

## RESULTS AND APPLICATIONS

Since this text is basically a catalogue, we have largely confined the discussion under each character to the reasoning behind the phyletic conclusions. These results are summarized in pictorial character state trees with familial distributions indicated. We could not entirely resist interpreting some of the findings in respect to current problems in taxonomic grouping or pointing out obvious functional and ecological correlations among characters. It is evident in many of the character state trees that the elapid-hydrophiid patterns of variation and change are often opposed or in contrast to those of viperines and crotalines. Further analysis can focus on such questions, or on the relations of individual lower taxa, posed in the setting of the vast array of variation among the Colubroidea. We have already pursued the latter course with *Azemiops,* one of the problem genera, using additional anatomical materials to more fully specify the relationships of this primitive form to the other viperids (Liem et al., 1971). It is patent that the materials generated by the present study are also broadly applicable in studying morphologic systems, ecological adaptations, or geographic patterns of distribution. One such study has been completed (Rabb and Marx, in press).

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# CHARACTERS

## Character 1—Dorsal Head Scalation

### Description of Character

The dorsum of the head is covered with shields. In the Colubroidea, there are usually nine large head shields: anteriorly a pair of internasals, followed by a pair of prefrontals, followed by a pair of supraoculars separated by a frontal, and posteriorly a pair of parietals. The arrangement of the head shields was used in literature on serpents even before Linnaeus. Although it is obvious that the several head scales have various independent attributes (e.g., keeling) and apparently exclusive properties (only large supraoculars or nasals may show raised, hornlike projections), the characteristic patterns of relations among the scales is our concern here.

Five states are recognized (Marx and Rabb, 1970, fig. 1):

State I — 9 head shields
State II — some large shields, some small scales
State III— all small head scales
State IV — fewer than 9 head shields
State V — intraspecific variation between States I and IV

State IV contains several classes, such as patterns with a single internasal, no internasals (fused with adjacent shields?), a single prefrontal, or absence of prefrontals and absence of the supraoculars. The frontal shield and the parietal shields were never found involved in an apparent reduction from the standard nine plate condition. We have treated any arrangement of fewer than the standard nine shields as belonging to this single state.

### Familial Ranges of Variation (Table 1)

Colubridae—This family has States I, II, IV, and V in a sample of 1,005 species of 201 genera. State I occurs in 837 species of 163 genera; II in 4 species of 2 genera (*Spalerosophis* is contained in *Zamenis* in Boulenger's Catalogue I); IV in 98 species of 26 genera; V in 66 species of 10 genera.

TABLE 1. Distribution of character states of dorsal head scalation.

| STATES | IV | V | I | II | III | I & II |
|---|---|---|---|---|---|---|
| Description | Less than nine dorsal head shields | Intraspecific variation between States I & IV | Nine large dorsal head shields | Fragmentation of some of the nine dorsal head shields | All dorsal head scales small | |
| | | | SPECIES | | | |
| Colubridae—1005[1] | 9.8% | 6.6% | 83.3% | 0.4% | | |
| Elapidae—139[1] | 0.7 | | 99.3 | | | |
| Hydrophiidae—42[2] | 2.4 | | 69.0 | 23.8 | | 4.8% |
| Viperinae—38 | | | 15.8 | 23.7 | 60.5% | |
| Crotalinae—45 | | | 20.0 | 80.0 | | |
| *Azemiops*—1 | | | 100.0 | | | |
| *Atractaspis*—16[5] | | | 100.0 | | | |
| | | | GENERA | | | |
| Colubridae—201[1] | 12.9 | 5.0 | 81.1 | 1.0 | | |
| Elapidae—29[1] | 3.4 | | 96.6 | | | |
| Hydrophiidae—16[2] | | | 62.5 | 18.8 | | 12.5[3] |
| Viperinae—8[4] | | | 12.5 | | 62.5 | |
| Crotalinae—6 | | | 16.7 | 66.7 | | 16.7 |
| *Azemiops*—1 | | | 100.0 | | | |
| *Atractaspis*—1 | | | 100.0 | | | |

[1]=Boulenger, 1893–96.
[2]=M. A. Smith, 1926, 1931.
[3]=plus *Aipysurus* (I, II, IV).
[4]=Intrageneric variation in *Atheris* and *Vipera* (II and III).
[5]=Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Elapidae—This family has States I and IV in a sample of 139 species and 29 genera. State I occurs in 138 species of 28 genera; IV is present in one species of a monotypic genus.

Hydrophiidae—The sea snakes have States I, II, and IV in a sample of 42 species of the 16 genera. State I occurs in 29 species and 10 genera; II in 10 species and 3 genera; IV in one species.

Intrageneric variation occurs in three genera: *Aipysurus* (I, II, IV); *Emydocephalus, Laticauda* (I, II). Intraspecific variation occurs in *Aipysurus eydouxii* and *Emydocephalus ijimae* (I and II).

In the Hydrophiidae, 61.9 per cent of the species (50.0 per cent of the genera) have the nasal shields continuous with the internasals, which is coded as State I in this text, whereas it was coded as State IV in Marx and Rabb, 1970.

Viperinae—The true vipers have States I, II, and III in a sample of 38 species of the 8 genera. State I occurs in 6 species of *Causus*; II in 9 species of 2 genera; III in 23 species of 7 genera.

Intrageneric variation occurs in two genera (*Atheris, Vipera*—II and III).

Crotalinae—The pit vipers have States I and II in a sample from 45 species of the 8 genera. State I occurs in 9 species and 2 genera; II in 36 species and 5 genera.

Intrageneric variation occurs in *Agkistrodon*.

*Azemiops* and *Atractaspis* have State I.

### Phyletics of Character 1

Character States II, IV, and V are rare in the colubrids (table 1) (Criterion 2).

State IV, fewer than nine head plates, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Apostolepis ambinigra*
- *Aspidura trachyprocta*
- *Calamaria leucogaster*
  - *linnaei*
  - *pavimentata*
  - *schlegeli*
  - *septentrionalis*
- *Chilorhinophis carpenteri*
- *Conophis lineatus*
  - *nasus*
- *Dimades plicatilis*
- *Enhydris bocourti*
  - *chinensis*
  - *enhydris*
  - *plumbea*
- *Farancia abacura*
- *Haldea striatula*

*Helicops angulatus*
  *carinicauda*
  *leopardinus*
  *schistosus*
*Hydraethiops melanogaster*
*Hydrops triangularis*
*Limnophis bicolor*
*Liodytes alleni*
*Macrocalamus lateralis*
*Opisthotropis kuatunensis*
  *latouchi*
*Prosymna ambigua*
*Tretanorhinus mocquardi*
Elapidae
  *Ultrocalamus preussi*

Colubrids with this character state show a higher frequency of occurrence in derived states of 15 other characters compared to the total colubrid working sample (table 2) (Criterion 3).

Also, these colubrids have a markedly large proportion of species of aquatic and fossorial habitats (53.3 per cent, 30.0 per cent), compared to the relative abundance of aquatic and fossorial colubrid species in the total working sample (14.9 per cent, 12.4 per cent—table 3) (Criterion 5).

TABLE 2. Correlation of States II and IV of Character 1 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters— | | |
|---|---|---|---|
| | In species having State II of Character 1 | In species having State IV of Character 1 | In total working sample |
| 2 | 75.0% (4)* | | 15.6% (31) |
| 5 | | 16.7% ( 4) | 3.5 ( 9) |
| 7 | 41.7 (3) | 53.3 (11) | 25.5 (56) |
| 9 | 58.3 (5) | 24.1 ( 3) | 6.8 (14) |
| 12 | 66.7 (6) | | 4.8 (13) |
| 14 | 41.7 (3) | | 3.5 ( 7) |
| 16 | 75.0 (5) | | 21.7 (34) |
| 17 | 75.0 (5) | | 35.4 (48) |
| 19 | | 90.0 (16) | 36.8 (68) |
| 22 | | 36.7 ( 7) | 4.5 (11) |
| 25 | | 47.4 ( 7) | 6.3 (12) |
| 28 | | 32.0 ( 5) | 11.7 (26) |
| 29 | | 18.5 ( 5) | 10.1 (27) |
| 31 | 33.3 (4) | 34.6 ( 7) | 19.5 (44) |
| 32 | | 71.4 (12) | 26.3 (55) |
| 34 | | 18.2 ( 4) | 6.8 (18) |
| 36 | | 14.3 ( 4) | 6.1 (16) |
| 38 | 33.3 (2) | | 16.2 (27) |
| 39 | | 26.3 ( 3) | 9.0 (15) |
| 40 | 41.7 (3) | | 24.8 (54) |
| 41 | | 25.0 ( 3) | 10.9 (20) |
| 42 | | 56.3 ( 7) | 8.7 (14) |
| 48 | 45.5 (3) | | 6.2 (11) |

* Number of genera.

TABLE 3. Habitat distribution of colubrid species having States II and IV of Character 1 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 1 % | State IV Character 1 % |
|---|---|---|---|
| Terrestrial | 36.2 | 83.3 | |
| Arboreal | 16.5 | | |
| Aquatic | 14.9 | 8.3 | 53.3 |
| Subterrestrial | 10.8 | | 16.7 |
| Fossorial | 12.4 | 8.3 | 30.0 |
| Variation | 5.3 | | |
| Unknown | 3.5 | | |

The aquatic colubrids tend to have their nostrils in a dorsal position, apparently for more effective air intake at the surface of the water. This is striking in the marine sea-snakes (Hydrophiidae), for 15 of 16 genera have their nostrils in a dorsal position and many have nasals fused with the internasals. Also, the fossorial snakes that use their heads as a blunt instrument for pushing into substrate tend to have a reduction or loss of other head plates (i.e., loreal or anterior temporals—table 4) (Criterion 4).

TABLE 4. Distribution of secretive colubrid and elapid species with fewer than nine dorsal head plates (State IV) with respect to loreal shield and anterior temporal scales.

| | | Anterior temporal | | | |
|---|---|---|---|---|---|
| | | 2 or 3 scales | 1 or 2 scales | 1 scale | absent |
| loreal | present | | | 1 | |
| | present or absent | 2 | | | |
| | absent | | 1 | 6 | 7 |

The application of four criteria (2, 3, 4, 5) suggests that State IV is derived.

That State IV arose from State I is directly suggested by the intraspecific variation between these two states (State V). Our working sample contained the following colubrids having State V: *Brachyorrhus albus*, *Carphophis amoena*, and *Ficimia publia*.

State II, fragmentation of some of the nine dorsal head shields, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Homalopsis buccata*
  - *Lystrophis d'orbignyi*
    - *semicinctus*
  - *Pituophis deppei*
    - *melanoleucus*
    - *sayi*
  - *Pythonodipsas carinata*
  - *Scaphiophis albopunctatus*
  - *Spalerosophis diadema*
- Hydrophiidae
  - *Acalyptophis peronii*
  - *Aipysurus duboisii*
    - *foliosquama*
    - *fuscus*
    - *laevis*
  - *Kolpophis annandalei*
  - *Laticauda colubrina*
    - *schistorhynchus*
    - *semifasciata*
  - *Thalassophis anomalus*
- Viperinae
  - *Atheris superciliaris*
  - *Vipera ammodytes*
    - *aspis*
    - *berus*
    - *kaznakovi*
    - *latasti*
    - *russelii*
    - *ursinii*
    - *xanthina*
- Crotalinae
  - *Agkistrodon hypnale*
    - *nepa*
  - *Bothrops* (11 species)
  - *Crotalus* (2)
  - *Lachesis mutus*
  - *Trimeresurus* (10)

The colubrids with this character state show a higher incidence in derived states of 11 other characters, compared to the frequency distribution of the total working sample (table 2) (Criterion 3).

Also these colubrids have a proportionately larger number of species assigned to the terrestrial habitat category (83.3 per cent) than does the total working sample (36.2 per cent—table 3) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State II is derived (Criterion 8).

State II probably arose in a different sequential direction from IV (plus V), for taxa possessing these states occur mostly in derived states of different characters (Table 2) and are predominantly abundant in different habitat zones (Table 3).

State III, all dorsal head scales small, does not occur in the colubrids (table 1). The taxa of Viperinae having State III are as follows:

- Viperinae
  - *Adenorhinos barbouri*
  - *Atheris ceratophorus*
    - *chlorechis*
    - *hindii*
    - *hispidus*
    - *katangensis*
    - *nitschei*
    - *squamiger*
  - *Bitis* (8)
  - *Cerastes* (2)
  - *Echis* (2)
  - *Eristicophis macmahoni*
  - *Vipera lebetina*
    - *persica*

TABLE 5. Enlarged dorsal head shields in *Vipera*.

| | Parietals | Frontal | Prefrontals | Internasals | Supraoculars |
|---|---|---|---|---|---|
| *V. berus* | + | + | P | P | + |
| *V. kaznakovi* | + | + | P | P | + |
| *V. ursini* | P | + | P | P | + |
| *V. xanthina* | O | O | O | P | + |
| *V. ammodytes* | O | O | O | O | + |
| *V. aspis* | O | O | O | O | + |
| *V. latasti* | O | O | O | O | + |
| *V. russeli* | O | O | O | O | + |
| *V. lebetina* | O | O | O | O | O/+ |
| *V. persica* | O | O | O | O | O |

KEY: O—fragmented small, keeled scales
+—large single shield (in pairs except frontal)
P—partly fragmented into smaller scales but distinguishable

We apply the uniqueness criterion (1) to State III, for its presence is unique to a derived stock.

State III probably arose from State II, which is intermediate between a full complement of nine head shields (State I) and a head covered by small scales (State III). The intermediacy is well illustrated in the genus *Vipera* (table 5). The presence of State II in the colubrids, viperines, and crotalines, and the absence of State III in the colubrids and its unique presence in the viperines, clearly supports a more highly derived condition for State III.

Our interpretation of the phyletics of Character 1 is shown in Figure 1.

## Character 2—Rostral Shield

### DESCRIPTION OF CHARACTER

The rostral shield is the median shield at the tip of the snout. It forms the anterior upper lip of the mouth (Peters, 1964, p. 306).

Four states of rostral shield scalation are recognized:

State I — single and rounded
State II — single, large, and modified
State III— intraspecific variation, States II and IV present in a species.
State IV — fragmented into several scales.

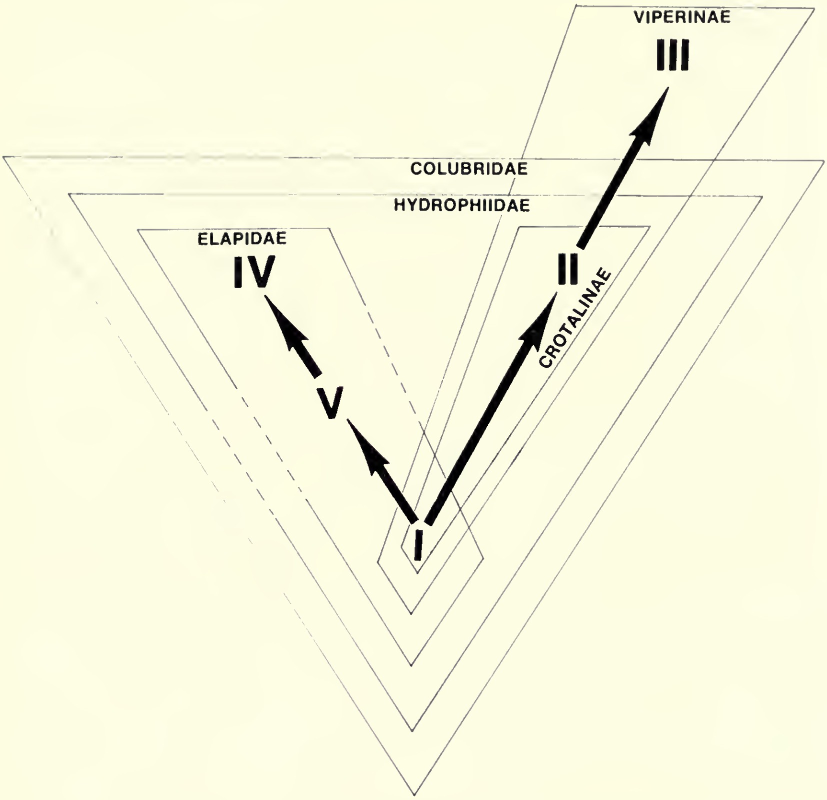

FIG. 1. Distribution among families of states of Character 1. Direction of change among states shown by arrows. Absence of a state in a family is indicated by a broken boundary.

### FAMILIAL RANGES OF VARIATION (Table 6)

Colubridae—This family has all four states in a sample of 972 species of 199 genera. State I occurs in 891 species of 165 genera, II in 76 species of 30 genera, III occurs in 2 species of the genus *Passerita,* IV occurs in 3 species of the genera *Langaha* and *Herpeton.*

Intrageneric variation in our "working sample" was observed in *Holarchus, Malpolon,* and *Uromacer* (States I and II).

Elapidae—This family has States I and II in a sample of 139 species of 30 genera. State I occurs in 130 species of 30 genera, II in 9 species of 5 genera.

Hydrophiidae—The sea snakes have States I, II and IV in a sample of 42 species of 16 genera. State I occurs in 39 species of 14 genera, II in 2 species of *Emydocephalus,* IV in the monotypic genus *Thalassophis.*

Viperinae—The true vipers have all four states in a sample of 38 species of the 8 genera. State I occurs in 29 species of 8 genera, II occurs in 6 species of *Causus,* III occurs in 3 *Vipera* (*latasti, ammodytes, aspis*), IV occurs only in *Vipera persica.*

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 28 species of 6 genera, II in 17 species of 3 genera. Intrageneric variation is present in 3 genera (*Agkistrodon, Bothrops, Trimeresurus*).

*Azemiops* and *Atractaspis* both have only State I.

## PHYLETICS OF CHARACTER 2

In the Colubridae, the rare states are those for modified or fragmented rostrals (States II, III, IV) (Criterion 2) (table 6).

State II, single and modified rostral, occurs in the following 49 colubrids in our working sample (plus other taxa):

- Colubridae
  - *Apostolepis ambinigra*
  - *Arizona elegans*
  - *Calamelaps unicolor*
  - *Chilomeniscus cinctus*
    - *fasciatus*
  - *Conophis lineatus*
  - *Conopsis lineatus*
    - *nasus*
  - *Ficimia publia*
  - *Gonyosoma oxcephalum*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Holarchus cyclurus*
  - *Hypsirhynchus ferox*
  - *Lioheterodon madagascariensis*
  - *Lystrophis d'orbignyi*
    - *semicinctus*
  - *Lytorhynchus diadema*
    - *maynardi*
  - *Macrocalamus lateralis*
  - *Malpolon moilensis*
  - *Oxybelis aeneus*
    - *argenteus*
    - *brevirostris*
    - *fulgidus*
  - *Passerita mycterizans*
    - *nasuta*
    - *prasinus*
  - *Phyllorhynchus decurtatus*
  - *Pituophis deppei*
    - *melanoleucus*
    - *sayi*
  - *Prosymna ambigua*
  - *Pseudaspis cana*
  - *Rhamphiophis oxyrhynchus*
  - *Rhinobothryum bovalli*
  - *Rhinocheilus lecontei*
  - *Rhinostoma guianense*
  - *Salvadora bairdi*
    - *grahami*
    - *hexalepis*
    - *lemniscata*
    - *lineata*
    - *mexicana*
  - *Scaphiophis albopunctatus*
  - *Stenorhina degenhardti*
  - *Tantilla gracilis*
  - *Uromacer oxyrhynchus*
- Elapidae
  - *Aspidelaps lubricus*
    - *scutatus*
  - *Brachyurophis semifasciatus*

TABLE 6. Distribution of character states of the rostral.

| | STATES | | | | | |
|---|---|---|---|---|---|---|
| | I | II | III | IV | INTRAGENERIC VARIATION | |
| Description | Round | Single & Modified | States II & IV | Fragmented | I, II | I, III, IV |
| | | | SPECIES | | | |
| Colubridae[1] —972 | 91.7% | 7.8% | 0.2% | 0.3% | | |
| Elapidae[1] —139 | 93.5 | 6.5 | | | | |
| Hydrophiidae[2] — 42 | 92.9 | 4.8 | | 2.4 | | |
| Viperinae[3] — 38 | 73.7 | 15.8 | 7.9 | 2.6 | | |
| Crotalinae[3] — 45 | 62.2 | 37.8 | | | | |
| *Azemiops*[3] — 1 | 100.0 | | | | | |
| *Atractaspis*[4] — 16 | 100.0 | | | | | |
| | | | GENERA | | | |
| Colubridae —199 | 82.9 | 15.1 | 0.5 | 1.0 | 0.5% | |
| Elapidae — 30 | 83.3 | 16.7 | | | | |
| Hydrophiidae — 16 | 87.5 | 6.3 | | 6.3 | | |
| Viperinae — 8 | 75.0 | 12.5 | | | | 12.5% |
| Crotalinae — 6 | 50.0 | | | | 50.0 | |
| *Azemiops* — 1 | 100.0 | | | | | |
| *Atractaspis* — 1 | 100.0 | | | | | |

[1] Data from Boulenger's Catalogues I, II, and III.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

  - *Hemachatus haemachatus*
- Viperinae
  - *Causus defilippii*
    - *lichtensteini*
    - *lineatus*
    - *resimus*
    - *rhombeatus*
- Hydrophiidae
  - *Emydocephalus annularis*
    - *ijimae*
- Crotalinae
  - *Agkistrodon acutus*
  - *Bothrops alternatus*
    - *atrox*
    - *barnetti*
    - *dunni*
    - *godmani*
    - *jararacussu*
    - *lansbergii*
    - *nummifer*
    - *schlegeli*
  - *Trimeresurus flavoviridis*
    - *jerdoni*
    - *mucrosquamatus*
    - *okinavensis*
    - *puniceus*
    - *stejnegeri*
    - *wagleri*

Modified rostrals in many colubrid and elapid taxa represent an adaptation for moving earth, as noted under Character 25 (Criterion 4).

These colubrids have a significantly larger proportion of species assigned to fossorial habitats (26.5 per cent) compared to the abundance of such species in the total sample (12.4 per cent) (Criterion 5) (table 7).

The application of three criteria (2, 4, 5) suggests that this state is derived (Criterion 8).

A fragmented rostral (State IV) is extremely rare in the colubrids (Criterion 2). G. A. Boulenger (1893) recorded only *Langaha* and *Herpeton* as having fragmented rostrals. These two genera are of different habitats (arboreal and aquatic) and occur in different geographic zones (Madagascar and Southeast Asia). Speculation has it that their rostral appendages may be tactile organs. State IV otherwise occurs in our sample in a single hydrophiid (*Thalassophis*

TABLE 7. Habitat distribution of colubrid species having State II of Character 2 compared to the total colubrid working sample.

| | Total working Sample | State II Character 2 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 34.7 |
| Arboreal | 16.5 | 18.4 |
| Aquatic | 14.9 | |
| Subterrestrial | 10.8 | 8.2 |
| Fossorial | 12.4 | 26.5 |
| Variation | 5.3 | 12.2 |
| Unknown | 3.5 | |

TABLE 8. Distribution of character states of the nasal shield's position to shields of the lip region.

| Description | STATES<br>I<br>Nasal in contact with rostral and supralabials | <br>II<br>Nasal separated from either rostral or supralabials | <br>III<br>Nasal separated from rostral and supralabials | |
|---|---|---|---|---|
| | | SPECIES | | VARIATION |
| Colubridae —380[1] | 99.0% | 1.0% | | |
| Elapidae — 90[1] | 100.0 | | | |
| Hydrophiidae— 42[2] | 100.0 | | | |
| Viperinae — 38[3] | 28.9 | 36.8 | 34.2% | |
| Crotalinae — 45[3] | 91.1 | 6.7 | | 2.2% |
| *Azemiops* — 1[3] | 100.0 | | | |
| *Atractaspis* — 13[4] | 100.0 | | | |
| | | GENERA | | |
| Colubridae —244 | 98.0 | 2.0 | | |
| Elapidae — 40 | 100.0 | | | |
| Hydrophiidae— 16 | 100.0 | | | |
| Viperinae — 8 | 12.5 | 12.5 | 37.5 | 37.5 |
| Crotalinae — 6 | 66.7 | | | 33.3 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

[1] Suite of references.
[2] M. A. Smith, 1926, 1931.
[3] Working sample.
[4] Laurent, 1950.

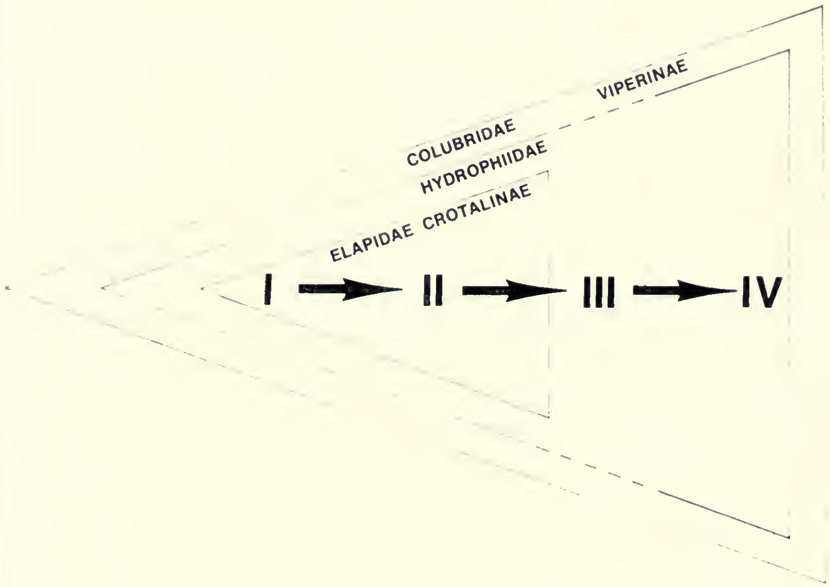

FIG. 2. Distribution among families of states of Character 2. Direction of change among states shown by arrows.

*anomalus*) and a single viper (*Vipera persicus*). With such extreme rarity in all stocks we designate this state as a derived condition.

State III, variation between an enlarged rostral and a fragmented condition, is also extremely rare, occurring in the colubrid genus *Passerita* (G. A. Boulenger, 1896), and three species of the genus *Vipera* (*ammodytes, aspis, latasti*). State III is by definition an intermediate sequential state between II and IV.

Although it is possible that State IV might be directly derived from State I, the existence of intermediate states suggests that this is not the case. Our interpretation of the phyletics of Character 2 is shown in Figure 2.

## Character 3—Position of Nasal Shield

### DESCRIPTION OF CHARACTER

The nasal shield is the head scale that contains the nostril. The nasal's contact with the rostral or the nasal's contact with the supralabials are not treated as separate characters. The close association of rostral and supralabials is evident from the almost universal contact with the nasal and their topographic proximity. From a devel-

TABLE 9. Intraspecific variation of relation of nasal scale to rostral and supralabials in *Bothrops nummifer*.

| Rostral | Supralabials | No. of specimens |
|---|---|---|
| + | + | 32 |
| +/0 | + | 1 |
| +/0 | +/0 | 1 |
| + | 0 | 1 |
| +/0 | 0 | 2 |
| 0 | + | 7 |
| 0 | +/0 | 3 |
| 0 | 0 | 2 |
|  |  | 49 |

KEY: + = contact.
0 = separated.
+/0 = individual variation.

opmental standpoint, they are probably serial homologues. This close relationship is illustrated by the intraspecific variation in *Bothrops nummifer* (table 9).

Three states are recognized:

State I — nasal in contact with rostral and supralabials.
State II — nasal separated from rostral, in contact with supralabials or in contact with rostral, separated from supralabials.
State III— nasal separated from rostral and supralabials.

### FAMILIAL RANGES OF VARIATION (Table 8)

Colubridae—This family has States I and II in a sample of 380 species of 244 genera. State I occurs in 376 species of 240 genera, II in 4 species of 4 genera.

Elapidae—This family only has State I in a sample of 90 species of 40 genera.

Hydrophiidae—The sea snakes only have State I in a sample of 42 species of 16 genera.

Viperinae—The true vipers have all three states in a sample of 38 species of the 8 genera. State I occurs in 11 species of 4 genera, II in 14 species of 3 genera, III in 13 species of 5 genera.

Intrageneric variation between States I and II occurs in *Atheris*, between States I and III in *Bitis*, and between I, II, and III in *Vipera*.

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 41 species of 6 genera, II in 3 species of *Crotalus* (*mitchelli, molossus,* and *ruber*).

Intrageneric variation occurs in *Bothrops* and *Crotalus*. Intraspecies variation occurs in *Bothrops nummifer*.

*Azemiops* and *Atractaspis* have State I.

## PHYLETICS OF CHARACTER 3

The colubrids almost always have the nasal shields in direct contact with the rostral and always with the supralabials. The nasal may be separated from the rostral by an internasal but never are there intervening small scales. The nasal is always in contact with the first supralabial or the first and/or second supralabials. Whether it is in contact with any of the supralabials posterior to the first supralabial depends on the relative sizes of the supralabials and nasal. There are no small scales intervening between the nasal and the supralabials in this family. Even in the two genera of colubrids that have multiple loreal scales (*Spalerosophis* and *Ptyas*; Character 7) the nasals are in broad contact with the supralabials and rostral.

State II, the separation of the nasal from the rostral by intervening internasals (Criterion 2) occurs very rarely in the Colubridae.

The six taxa of colubrids having State II as sampled from our Suite of References and working sample are:

*Ficimia publia*
*Hypoptophis wilsoni*
*Melanocalamus leopoldi*
*Miodon collaris*
*Polemon bocourti*
*Stenorhina degenhardti*

These are all fossorial and subterrestrial snakes (Criterion 5). See discussion of Character 1 for modification of head shields for burrowing.

In the Viperidae (Viperinae and Crotalinae) all three states occur. There are intervening scales between the nasal and the rostral and/or supralabials. Possession of these scales about the nasal presumably allows more mobility at the surface for the nasal chamber and its opening. This may be advantageous in respect to (1) orienting for olfaction, (2) orienting and closing the nostrils in the face of sand and dust, and/or (3) movement necessary in non-olfactory functions of the nasal and supranasal chambers (hissing and thermal gradient detection). The first seems the least likely explanation, for, if so, similar developments would presumably have been advantageous to

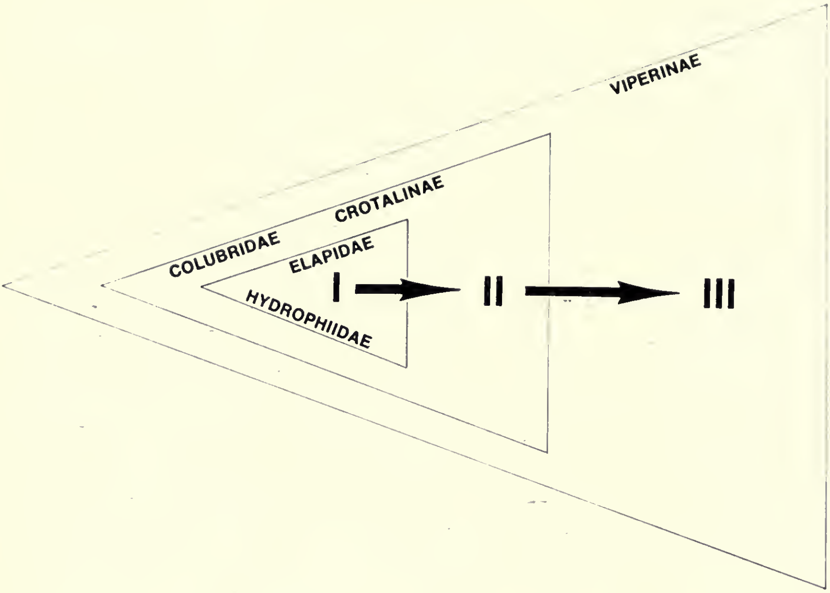

FIG. 3. Distribution among families of states of Character 3. Direction of change among states shown by arrows.

many colubrids. To a lesser extent, this objection also seems to hold for the second possibility. The third alternative has anatomical correlations peculiar to the viperines, but functional studies are lacking.

States II and III are considered derived because of their extreme rarity or absence in the colubrid stock (Criteria 1 and 2). In addition, special adaptation to a particular mode of life is indicated for State II (Criterion 5), and there are possible functional adaptations correlated with State III in the true vipers (Criterion 4).

The logical structural course in separation of the nasal from the mouth rim would be gradual interpolation of other scales. This is apparently the course taken in the vipers, as shown by the intrageneric variation. We therefore interpret the phyletics of Character 3 as shown in Figure 3.

## Character 4—Nasal Shield Depression

### DESCRIPTION OF CHARACTER

The posterior area of the nasal shield may have an exposed semicircular depression (Marx and Rabb, 1965, p. 182, fig. 41C).

TABLE 10. Distribution of character states of the nasal shield depression.

| Description | | STATES<br>I<br>Absent | <br>II<br>Present |
|---|---|---|---|
| | SPECIES | | |
| Colubridae[1] | —314 | 96.2% | 3.8% |
| Elapidae[2] | — 88 | 100.0 | |
| Hydrophiidae[3] | — 42 | 100.0 | |
| Viperinae[1] | — 38 | 97.4 | 2.6 |
| Crotalinae[1] | — 46 | 100.0 | |
| *Azemiops*[1] | — 1 | 100.0 | |
| *Atractaspis*[4] | — 13 | 100.0 | |
| | GENERA | | |
| Colubridae | —165 | 97.6 | 2.4 |
| Elapidae | — 46 | 100.0 | |
| Hydrophiidae | — 16 | 100.0 | |
| Viperinae | — 8 | 87.5 | 12.5 |
| Crotalinae | — 6 | 100.0 | |
| *Azemiops* | — 1 | 100.0 | |
| *Atractaspis* | — 1 | 100.0 | |

[1] Working sample.
[2] Suite of references.
[3] M. A. Smith, 1926, 1931.
[4] Laurent, 1950.

Two states are recognized:

State I — depression absent
State II — depression present

### FAMILIAL RANGES OF VARIATION (Table 10)

Colubridae—This family has States I and II in a sample of 314 species of 165 genera. State I occurs in 302 species of 161 genera, II in 12 species of 4 genera.

Elapidae, Hydrophiidae, Crotalinae—All taxa in these three familial groups have State I as sampled in 176 species (88, 42, 46, respectively) of 67 genera (46, 15, 6).

Viperinae—The true vipers have States I and II in a sample of 38 species of the 8 genera. State I occurs in 37 species of 7 genera, II is restricted to the monotypic genus *Adenorhinos*.

*Azemiops* and *Atractaspis* have State I.

### PHYLETICS OF CHARACTER 4

State II, the presence of a nasal shield depression, occurs very rarely in the Colubridae (Criterion 2).

The 12 colubrid taxa having State II in our working sample are:

*Achalinus spinalis*
*Boiga blandingi*
  *cynodon*
  *dendrophilia*
  *irregularis*
  *jaspidea*
*Boiga kraepelini*
  *multimaculata*
  *pulverulentus*
  *trigonatus*
*Crotaphopeltis hotamboeia*
*Elachistodon westermanni*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 11) (Criterion 3).

Also, these colubrids have a markedly larger number of species in the arboreal habitat category (75.0 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent) (Criterion 5).

These colubrids also are all from part of the Old World: Africa, Asia, and Indo-Australia (Criterion 6), and 75 per cent are confined to a single genus (Criterion 7).

The application of five criteria strongly suggests that this state is derived (Criterion 8).

Our interpretation of the phyletics of Character 4 is shown in Figure 4.

## Character 5—Position of Nostril in Nasal Shield

### DESCRIPTION OF CHARACTER

The nostril (external naris) almost always lies within the nasal shield but may lie on the border of the nasal shield and an adjacent shield. The nostril varies in its position in the nasal shield (table 12).

TABLE 11. Correlation of State II of Character 4 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters— | | | |
|---|---|---|---|---|
| | In species having State II of Character 4 | | In total working sample | |
| 13 | 91.7% | (3)* | 31.8% | (54) |
| 20 | 75.0 | (3) | 41.2 | (74) |
| 21 | 75.0 | (1) | 18.9 | (29) |
| 31 | 75.0 | (2) | 19.5 | (44) |
| 33 | 75.0 | (2) | 43.0 | (76) |
| 46 | 83.3 | (2) | 26.9 | (52) |

* Number of genera.

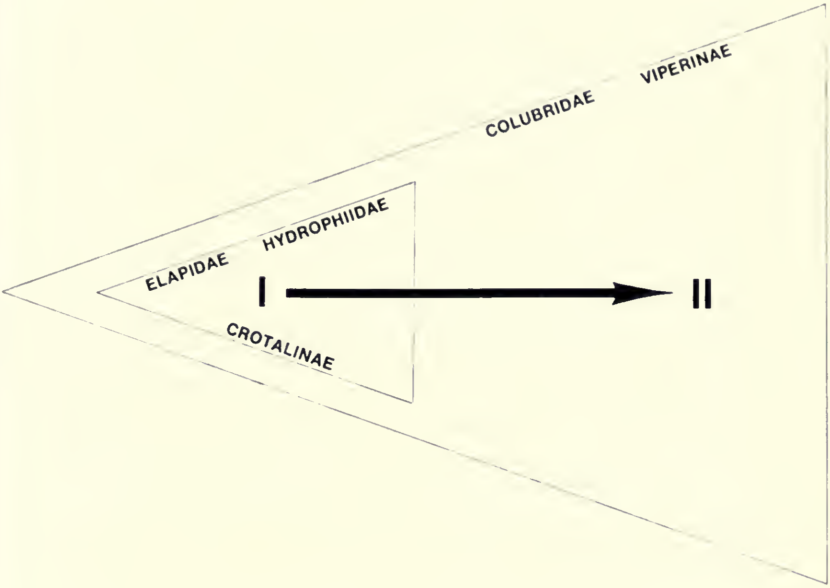

FIG. 4. Distribution among families of states of Characters 4 and 18. Direction of change among states shown by arrows.

Five states are recognized:

State I — medial
State II — anterior
State III— posterior
State IV — ventral
State V — dorsal

### FAMILIAL RANGES OF VARIATION (Table 12)

Colubridae—This family has all five states in a sample of 313 species of 164 genera. State I occurs in 301 species of 155 genera, State II in 7 species of 4 genera. State III occurs in 1 species of *Darlingtonia*. State IV is found in 2 species of 2 genera, as is State V.

Intrageneric variation is observed in *Arrhyton* (States I and II).

Elapidae—This family has States I, IV, and V in a sample of 69 species of 38 genera. State I occurs in 59 species of 34 genera. State IV occurs in the monotypic *Ogmodon*. State V occurs in 9 species of 3 genera.

Hydrophiidae—The sea snakes have States I, III, and V in a sample of 42 species of 16 genera. State I occurs in 19 species of 10

TABLE 12. Distribution of character states of the position of the nostril in the nasal.

| | STATES | | | | | | |
|---|---|---|---|---|---|---|---|
| Description | I<br>Medial | II<br>Anterior | III<br>Posterior | IV<br>Ventral | V<br>Dorsal | | |
| | | | SPECIES | | | | |
| Colubridae —313 | 96.2% | 2.2% | 0.3% | 0.6% | 0.6% | | |
| Elapidae — 69 | 85.5 | | | 1.4 | 13.0 | | |
| Hydrophiidae— 42 | 45.2 | | 52.4 | | 2.4 | | |
| Viperinae — 39 | 69.2 | 2.6 | 23.1 | | | | |
| Crotalinae — 45 | 95.6 | | 4.4 | | | | |
| *Azemiops* — 1 | 100.0 | | | | | | |
| *Atractaspis* — 13 | 61.5 | 38.5 | | | | | |
| | | | GENERA | | | INTRAGENERIC VARIATION | |
| | | | | | | I & II | I & III |
| Colubridae —164 | 94.5 | 2.4 | 0.6 | 1.2 | 1.2 | 0.6% | |
| Elapidae — 38 | 89.5 | | | 2.6 | 7.9 | | |
| Hydrophiidae— 16 | 56.3 | | 31.3 | | 6.3 | | 6.3% |
| Viperinae — 8 | 50.0 | 12.5 | 25.0 | | | | 12.5 |
| Crotalinae — 6 | 83.3 | | | | | | 16.7 |
| *Azemiops* — 1 | 100.0 | | | | | | |
| *Atractaspis* — 1 | | | | | | 100.0 | |

TABLE 13. Correlation of State II of Character 5 with derived states of certain other characters in Colubridae.

| | Frequency of derived states in indicated characters— | | | |
|---|---|---|---|---|
| Character | In species having State II of Character 5 | | In total working sample | |
| 7 | 71.4% | (3)* | 25.1% | (56) |
| 9 | 71.4 | (4) | 6.8 | (14) |
| 27 | 67.5 | (3) | 17.9 | (40) |
| 28 | 50.0 | (3) | 11.7 | (26) |
| 32 | 100.0 | (5) | 26.3 | (55) |
| 37 | 57.2 | (3) | 22.9 | (54) |

* Number of genera.

genera, State III in 22 species of 6 genera. State V occurs in the monotypic genus *Thalassophis.*

Intrageneric variation occurs in *Hydrophis,* which has States I and III.

Viperinae—The true vipers have States I, II, and III in a sample of 39 species of 8 genera. State I occurs in 25 species of 5 genera. State II occurs only in the monotypic genus *Adenorhinos.* State III occurs in 9 species of 3 genera.

Intrageneric variation occurs in the genus *Vipera,* which has States I and III.

Crotalinae—The pit-vipers have States I and III in a sample of 45 species of all 6 genera. State I occurs in 43 species of 6 genera. State II occurs in 2 species of *Crotalus.*

Intrageneric variation occurs only in *Crotalus.*

*Azemiops* has State I.

*Atractaspis* has States I and II (Laurent, 1950).

## PHYLETICS OF CHARACTER 5

State II, a nostril positioned anteriorly in the nasal, occurs rarely in the Colubridae (Criterion 2) (table 12). State II occurs in the following colubrids (plus other taxa):

*Arrhyton vittatum*
*Calamelaps unicolor*
*Conopsis lineatus*
  *nasus*
*Prosymna ambigua*
*Pseudorhabdion collaris*
  *longiceps*

Viperinae
  *Adenorhinos barbouri*

*Atractaspis* (5 species)

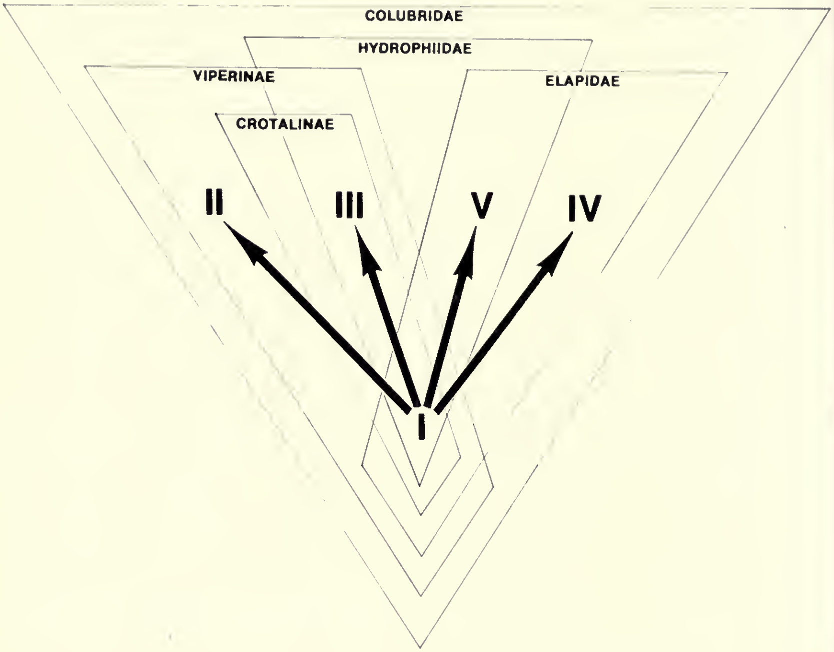

FIG. 5. Distribution among families of states of Character 5. Direction of change among states shown by arrows.

In the colubrids this feature has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same 6 characters in the total sample (table 13) (Criterion 3).

These colubrids are all in subterrestrial or fossorial habitat categories (Criterion 5).

The application of three criteria (2–3, 5) strongly suggests that this state is derived (Criterion 8).

States III, IV, and V also occur rarely in the working sample of the Colubridae (Criterion 2). The colubrids (plus other taxa) having these three states are as follows:

- State III
  - Colubridae—none
  - Hydrophiidae
    - *Astrotia stokesii*
    - *Ephalophis greyi*
    - *Hydrophis* (15 of 16 species)
    - *Lapemis curtis*
      - *hardwicki*
    - *Microcephalophis cantoris*
      - *gracilis*
    - *Pelamis platurus*
  - Viperinae
    - *Causus* (6 species)

    - *Eristicophis macmahoni*
    - *Vipera lebetina*
      - *russelii*
  - Crotalinae
    - *Crotalus atrox*
      - *mitchelli*
- State IV
  - Colubridae
    - *Chilorhinophis carpenteri*
    - *Macrocalamus lateralis*
  - Elapidae
    - *Ogmodon vitianus*
- State V
  - Colubridae
    - *Pythonodipsas carinatus*
    - *Rhinobothryum bovalli*
  - Elapidae
    - *Aspidelaps lubricus*
      - *scutatus*
    - *Hemachatus haemachatus*
    - *Naja flava*
      - *haje*
      - *melanoleuca*
      - *naja*
      - *nigricollis*
      - *nivea*
  - Hydrophiidae
    - *Thalassophis anomalus*

We consider each of these four rare states (II–V) as being separately derived from State I. State I represents a topographically central position; changing the site of the nostril in a single direction is probably less complex genetically and mechanically than progressing through several sites, and there is no evidence suggestive of the latter process.

Our interpretation of the phyletics of Character 5 is shown in Figure 5.

## Character 6—Supranasal Horns

### Description of Character

The supranasal shield or the scales between them may be raised to form a set of large supranasal horns.

Two states are recognized:

State I — horns absent
State II — horns present

### Familial Ranges of Variation (Table 14)

Colubridae, Elapidae, Crotalinae—All taxa in these three familial groups have State I as sampled in 1,187 species (1,003, 139, 45 respectively) of 245 genera (201, 38, 6).

Hydrophiidae—The sea snakes have States I and II. State I occurs in 37 species of 15 genera, II is restricted to the monotypic genus *Acalyptophis*.

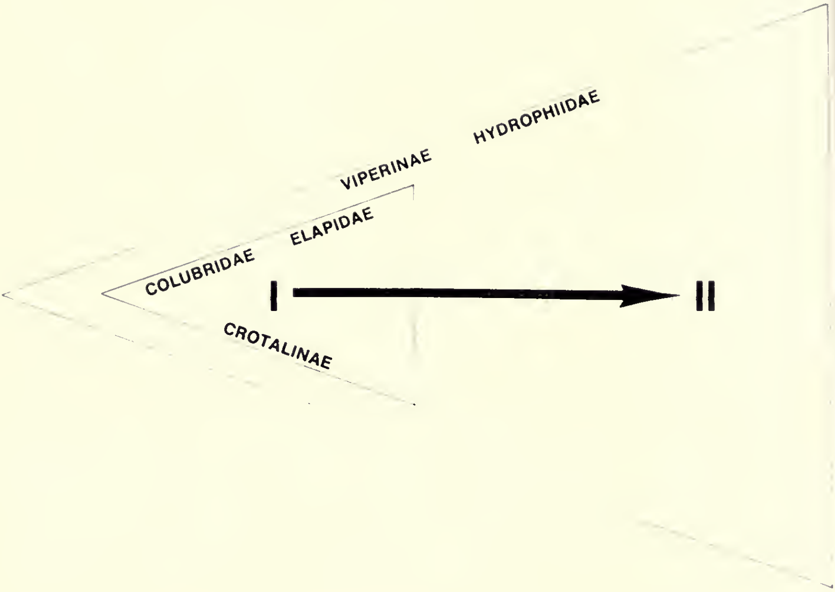

FIG. 6. Distribution among families of states of Character 6. Direction of change among states shown by arrows.

Viperinae—The true-vipers have States I and II. State I occurs in 33 species of 8 genera, II in two species of *Bitis* (*gabonica, nasicornis*).

Intrageneric variation occurs in *Bitis*.

*Azemiops* and *Atractaspis* have State I.

### PHYLETICS OF CHARACTER 6

State II does not occur in the ancestral colubrids and rarely occurs in some of its derived stocks. We apply the uniqueness criterion (1) to character State II, for its presence is unique to derived stocks.

Our interpretation of the phyletics of Character 6 is shown in Figure 6.

## Character 7—Loreal Shield

### DESCRIPTION OF CHARACTER

The loreal shield is the scale (or scales) separating the postnasal shield from the preocular shield. If the postnasal is in contact with the shield(s) that touch the eye (preocular or preoculars), we here define this condition as lacking a loreal.

TABLE 14. Distribution of character states of the supranasal horns.

| | | STATES | | |
|---|---|---|---|---|
| | | I | II | |
| Description | | Absent | Present | |
| | | SPECIES | | |
| Colubridae[1] | —1,003 | 100.0% | | |
| Elapidae[1] | — 139 | 100.0 | | |
| Hydrophiidae[2] | — 42 | 97.6 | 2.4% | |
| Viperinae[3] | — 35 | 94.3 | 5.7 | |
| Crotalinae[3] | — 45 | 100.0 | | |
| *Azemiops*[3] | — 1 | 100.0 | | |
| *Atractaspis*[4] | — 16 | 100.0 | | |
| | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | — 201 | 100.0 | | |
| Elapidae | — 38 | 100.0 | | |
| Hydrophiidae | — 16 | 93.7 | 6.3 | |
| Viperinae | — 8 | 87.5 | | 12.5% |
| Crotalinae | — 6 | 100.0 | | |
| *Azemiops* | — 1 | 100.0 | | |
| *Atractaspis* | — 1 | 100.0 | | |

[1] Boulenger, 1893–1896.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Three states are recognized:

State I — one to three loreals
State II — more than three loreals
State III— loreal absent

We have combined classes in State I because intraspecific variation of an additional loreal or two is infrequent and confined to the Colubridae (Table 15) (Peters, 1964).

### FAMILIAL RANGES OF VARIATION (Table 16)

Colubridae—This family has all three states in a sample of 993 species of 189 genera. State I occurs in 788 species of 160 genera, II in 4 species of 2 genera, III in 201 species of 27 genera.

Elapidae—This family only has State III in a sample of 138 species of 29 genera.

TABLE 15. Distribution of relative abundance of the number of loreals.

|  | Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3] | *Azemiops*[3] | *Atractaspis*[4] | Crotalinae[3] |
|---|---|---|---|---|---|---|---|
| Number of Species | 993 (189)[5] | 138 (29) | 42 (16) | 38 (8) | 1 | 16 | 45 (6) |
| Number of Loreals |  |  |  |  |  |  |  |
| 0 | 20.2% | 100.0% | 97.6% | 2.6% |  | 100.0% | 2.2% |
| 0–1[6] | 3.1 |  |  |  |  |  |  |
| 1 | 72.6 |  | 2.4 | 15.8 | 100.0% |  | 13.3 |
| 1–2 | 0.7 |  |  |  |  |  |  |
| 2 | 1.2 |  |  |  |  |  |  |
| 1–3 | 0.5 |  |  |  |  |  |  |
| 2–3 | 0.5 |  |  |  |  |  |  |
| 3 | 0.5 |  |  |  |  |  |  |
| 3–4 | 0.1 |  |  |  |  |  |  |
| 1–4 | 0.1 |  |  |  |  |  |  |
| 3 plus | 0.4 |  |  | 81.6 |  |  | 84.4 |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

[5] Number of genera.

[6] Intraspecific variation.

TABLE 16. Distribution of character states of the loreal shield.

| | | STATES | | | |
|---|---|---|---|---|---|
| | | III | I | II | |
| Description | | Absent | 1–3 | 3 plus | |
| | | | SPECIES | | |
| Colubridae[1] | —993 | 20.2% | 79.3% | 0.4% | |
| Elapidae | —138 | 100.0 | | | |
| Hydrophiidae | — 42 | 97.6 | 2.4 | | |
| Viperinae | — 38 | 2.6 | 15.8 | 81.6 | |
| Crotalinae | — 45 | 2.2 | 13.3 | 84.4 | |
| *Azemiops* | — 1 | | 100.0 | | |
| *Atractaspis* | — 16 | 100.0 | | | |
| | | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | —189 | 14.3 | 85.2 | 1.1 | |
| Elapidae | — 29 | 100.0 | | | |
| Hydrophiidae | — 16 | 93.7 | 6.3 | | |
| Viperinae | — 8 | 12.5 | 12.5 | 75.0 | |
| Crotalinae | — 6 | | 16.7 | 67.7 | 16.7% |
| *Azemiops* | — 1 | | 100.0 | | |
| *Atractaspis* | — 1 | 100.0 | | | |

[1] See Table 15.

Hydrophiidae—The sea snakes have States I and III in a sample of 42 species of 16 genera. State I occurs only in the monotypic genus *Kolpophis* (Voris, *personal communication*), III in 41 species of 15 genera.

Viperinae—The true vipers have all three states in a sample of 38 species of 8 genera. State I occurs in 6 species of *Causus*, II in 31 species of 6 genera, III only in the monotypic genus *Adenorhinos*.

Crotalinae—The pit vipers have all three states in a sample of 45 species of 6 genera. State I occurs in 6 species of 2 genera, II in 38 species of 5 genera, III only in *Agkistrodon strauchi*.

Intrageneric variation occurs in *Agkistrodon*, which has all three states.

*Azemiops* has State I.

*Atractaspis* has State III.

## Phyletics of Character 7

Character State III is not particularly rare in the colubrids (table 16). State III, absence of a loreal, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Abastor erythrogrammus*
  - *Achalinus spinalis*
  - *Aparallactus lunnulatus*
    - *werneri*
  - *Apostolepis ambinigra*
  - *Arrhyton taeniatum*
  - *Aspidura trachyprocta*
  - *Atractus elaps*
    - *erythromelas*
    - *latifrons*
    - *ventrimaculatus*
  - *Brachyorrhus albus*
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Carphophis amoena*
  - *Chilomeniscus cinctus*
    - *fasciatus*
  - *Chilorhinophis carpenteri*
  - *Cyclocorus lineatus*
  - *Darlingtonia haetiana*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Dimades plicatilis*
  - *Dipsadoboa unicolor*
  - *Dryocalamus davisoni*
  - *Elachistodon westermanni*
  - *Elapomorphus blumii*
  - *Farancia abacura*
  - *Ficimia publia*
  - *Geophis multitorques*
    - *semidoliatus*
  - *Haldea striatula*
  - *Hydrops triangularis*
  - *Lampropeltis elapsoides*
    - *triangulus*
  - *Leptophis occidentalis*
  - *Liopeltis tricolor*
  - *Macrocalamus lateralis*
  - *Miodon gabonensis*
  - *Ninia atrata*
    - *sebae*
  - *Opisthoplus degener*
  - *Opisthotropis latouchi*
  - *Oxybelis aeneus*
    - *brevirostris*
    - *fulgidus*
  - *Sibon sibon*
  - *Stilostoma extenuatum*
  - *Storeria dekayi*
    - *occipitomaculata*
  - *Tantilla gracilis*
  - *Telescopus iberus*
  - *Tomodon dorsatus*
  - *Trirhinopholis styani*
  - *Tropidodipsas fischeri*
- Elapidae—all 69 species
- Hydrophiidae—37 species (of 38)
- Viperinae—*Adenorhinos barbouri*
- Crotalinae—*Agkistrodon strauchi*

In these colubrids this character state has a higher frequency of correlation with derived states of 18 other characters compared to the frequency distribution of these states of the same 18 characters in the total sample (table 17) (Criterion 3).

These colubrids also have a markedly larger number of species of secretive habits (fossorial and subterrestrial—65 per cent) compared to the relative abundance of fossorial and subterrestrial colubrid species in the total sample (23.2 per cent) (table 18) (Criterion 5).

The application of two criteria suggests that this state is derived (Criterion 8).

TABLE 17. Correlation of State III of Character 7 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State III of Character 7 | In total working sample |
| 1 | 28.3% (13)* | 14.3% (28) |
| 9 | 22.0 (8) | 6.8 (14) |
| 13 | 51.7 (20) | 31.8 (54) |
| 19 | 64.4 (39) | 36.8 (68) |
| 22 | 16.7 (8) | 4.5 (11) |
| 25 | 15.4 (4) | 6.3 (12) |
| 28 | 36.7 (13) | 11.7 (26) |
| 29 | 33.3 (15) | 10.1 (27) |
| 30 | 14.9 (6) | 6.3 (15) |
| 32 | 52.3 (16) | 26.3 (55) |
| 34 | 24.0 (10) | 6.8 (18) |
| 36 | 20.7 (11) | 6.1 (16) |
| 38 | 44.4 (14) | 16.2 (27) |
| 39 | 20.0 (6) | 9.0 (15) |
| 40 | 40.0 (19) | 24.8 (54) |
| 42 | 31.4 (8) | 8.7 (14) |
| 44 | 16.7 (6) | 5.8 (11) |
| 50 | 35.0 (8) | 20.0 (24) |

* Number of genera.

State II, many loreals, is extremely rare in the Colubridae (table 16). In our working sample three colubrids have this state: *Ptyas mucosus, Pythonodipsas carinatus,* and *Spalerosophis diadema.* These three colubrids all have derived states of two other characters (17, 20) (Criteria 3).

TABLE 18. Habitat distribution of colubrid species having State III of Character 7 compared to the total colubrid working sample.

| | Total Working Sample | State III Character 7 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 10.0 |
| Arboreal | 16.5 | 18.3 |
| Aquatic | 14.9 | 5.0 |
| Subterrestrial | 10.8 | 28.3 |
| Fossorial | 12.4 | 36.7 |
| Variation | 5.3 | |
| Unknown | 3.5 | 1.7 |

The application of two criteria suggests that this state is derived (Criterion 8).

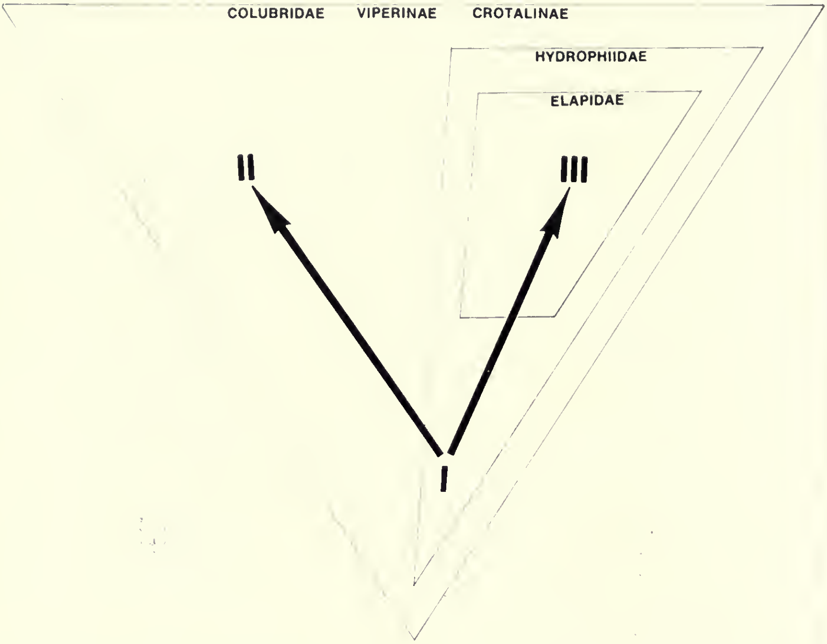

Fig. 7. Distribution among families of states of Character 7. Direction of change among states shown by arrows.

Within the Viperinae the almost universal condition is many loreal scales. A possible advantage of the many scale condition is that it facilitates movement in the area, particularly erection of the maxillary apparatus.

*Adenorhinos barbouri* is the only true viper that lacks a loreal. This probably reflects overall shortening of the anterior head region, which is also shown in the reduction of other head shields. This probably is a reversal from the multiple loreal condition through a reduction of the number of loreals.

Our interpretation is that States II and III arose in different directions because each state is overwhelmingly abundant in different families (table 15) (Criterion 7). Our interpretation of the phyletics of Character 7 is shown in Figure 7.

## Character 8—Supraocular Horns

### Description of Character

The supraocular scales may include one or several enlarged spine-like scale(s) which are referred to as supraocular horns.

Three states are recognized:

State I —horns absent
State II —intraspecific variation, both States I and III present
State III—horns present

### FAMILIAL RANGES OF VARIATION (Table 19)

Colubridae—All taxa have State I in a sample of 314 species of 163 genera (working sample).

Elapidae—This family has States I and II in a sample of 69 species of 38 genera. State I occurs in 68 species of 37 genera, II only in the monotypic genus *Acanthophis.*

Hydrophiidae—The sea snakes have States I and III in a sample of 42 species of 16 genera. State I occurs in 41 species of 15 genera, III in the monotypic genus *Acalyptophis.*

Viperinae—The true vipers have all three states in a sample of 37 species of 8 genera. State I occurs in 32 species in the 8 genera, II in two species of two genera, III in three species of three genera. Intraspecific variation occurs in two species and intrageneric variation occurs in three genera (*Vipera, Atheris, Bitis*).

Crotalinae—The pit vipers have all three states in a sample of 45 species of 6 genera. State I occurs in 43 species of the 6 genera, II in *Bothrops schlegeli,* III in *Crotalus cerastes.*

Intrageneric variation occurs in two genera (*Bothrops, Crotalus*).

*Azemiops* and *Atractaspis* have State I.

### PHYLETICS OF CHARACTER 8

States II and III do not occur in the ancestral colubrids and rarely in some of the derived stocks. The taxa that have supraocular horns are:

State II
- Elapidae
  - *Acanthophis antarticus*
- Viperinae
  - *Bitis cornutus*
  - *Cerastes vipera*
- Crotalinae
  - *Bothrops schlegeli*

State III
- Hydrophiidae
  - *Acalyptophis peronii*
- Viperinae
  - *Atheris ceratophorus*
  - *Bitis worthingtoni*
  - *Vipera persica*
- Crotalinae
  - *Crotalus cerastes*

TABLE 19. Distribution of character states of the supraocular horns.

| DESCRIPTION | STATES<br>I<br>ABSENT | <br>II<br>INTRASPECIFIC VARIATION | <br>III<br>PRESENT | INTRAGENERIC VARIATION |
|---|---|---|---|---|
| | | SPECIES | | |
| Colubridae —314[1] | 100.0% | | | |
| Elapidae — 69 | 99.6 | 1.4% | | |
| Hydrophiidae— 42 | 97.6 | | 2.4% | |
| Viperinae — 37 | 86.5 | 5.4 | 8.1 | |
| Crotalinae — 45 | 95.6 | 2.2 | 2.2 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 16 | 100.0 | | | |
| | | GENERA | | |
| Colubridae —163 | 100.0 | | | |
| Elapidae — 38 | 97.3 | 2.7 | | |
| Hydrophiidae— 16 | 93.7 | | 6.3 | |
| Viperinae — 8 | 50.0 | | | 50.0% |
| Crotalinae — 6 | 66.7 | | | 33.3 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

[1] Working sample.

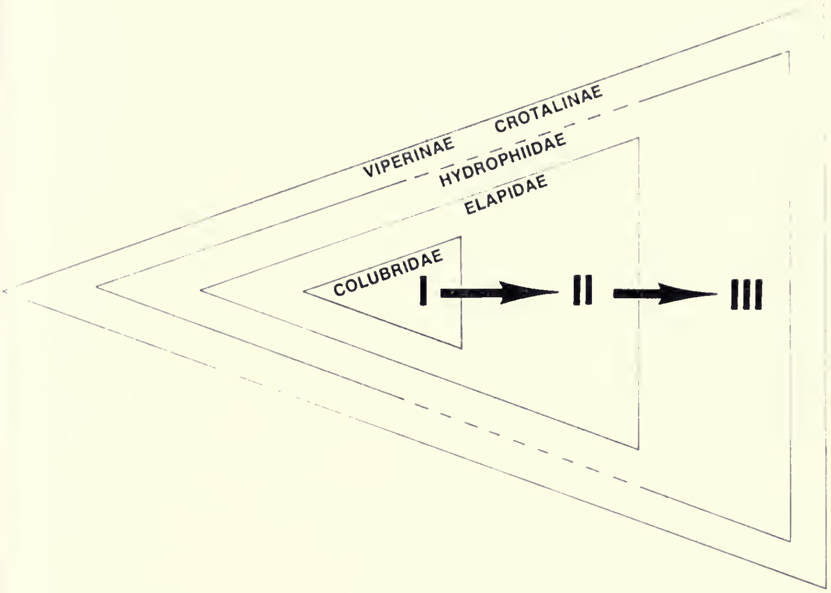

FIG. 8. Distribution among families of states of Character 8. Direction of change among states shown by arrows.

We apply the uniqueness criterion (1) to Character States II and III since its presence is unique to derived stocks.

State II is an intermediate sequential state because each taxon with this state has both states I and III.

Our interpretation of the phyletics of Character 8 is shown in Figure 8.

## Character 9—Anterior Temporal Shields

### DESCRIPTION OF CHARACTER

The anterior temporal shields are the scales posterior to and in contact with the postoculars. They separate the parietal from the supralabials (Peters, 1964).

Three states are recognized:

State I —one to three anterior temporals
State II —more than three anterior temporals
State III—anterior temporals absent; parietal in contact with supralabials

TABLE 20. Distribution of character states of the anterior temporals.

| | STATES | | | | |
|---|---|---|---|---|---|
| | III | I | II | | |
| Description | Absent | 1–3 | 3 plus | | |
| | | SPECIES | | INTRASPECIFIC VARIATION | |
| | | | | I & III | I & II |
| Colubridae[1] —990 | 8.5% | 89.9% | 1.3% | 0.2% | |
| Elapidae —132 | 1.5 | 98.5 | | | |
| Hydrophiidae— 47 | | 95.7 | 2.1 | | 2.1% |
| Viperinae — 35 | | 20.0 | 80.0 | | |
| Crotalinae — 45 | | 11.1 | 88.9 | | |
| *Azemiops* — 1 | | 100.0 | | | |
| *Atractaspis* — 14 | | 100.0 | | | |
| | | GENERA | | INTRAGENERIC VARIATION | |
| Colubridae —198 | 6.1 | 89.9 | 1.5 | 1.0 | 1.5 |
| Elapidae — 29 | 3.6 | 93.1 | | 3.6 | |
| Hydrophiidae— 15 | | 86.7 | 6.7 | | 6.7 |
| Viperinae — 8 | | 25.0 | 75.0 | | |
| Crotalinae — 6 | | | 83.3 | | 16.7 |
| *Azemiops* — 1 | | 100.0 | | | |
| *Atractaspis* — 1 | | 100.0 | | | |

[1] See Table 23.

## FAMILIAL RANGES OF VARIATION (Table 20)

Colubridae—This family has all three states in a sample of 990 species of 198 genera. State I occurs in 891 species of 178 genera, II in 13 species of 3 genera, III in 84 species of 12 genera.

Intraspecific variation occurs in 2 species, and intrageneric variation in 5 genera.

Elapidae—This family has States I and III in a sample of 132 species of 29 genera. State I occurs in 130 species of 27 genera, III in 2 species of 2 genera.

Intrageneric variation occurs in *Hemibungarus*.

Hydrophiidae—The sea snakes have States I and II in a sample of 47 species of 15 genera. State I occurs in 45 species of 13 genera, State II in monotypic *Kolpophis*.

Intraspecific variation occurs in *Aipysurus laevis*. Intrageneric variation in *Aipysurus*.

Viperinae—The true vipers have States I and II in a sample of 35 species in the 8 genera. State I occurs in 7 species of 2 genera, II in 28 species of 6 genera.

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 5 species of *Agkistrodon,* II in 40 species of 6 genera.

Intrageneric variation occurs in *Agkistrodon.*

*Azemiops* and *Atractaspis* have State I.

### PHYLETICS OF CHARACTER 9

Character state III is rare in the colubrids (table 20).

State III, absence of anterior temporals, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Apostolepis ambinigra*
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Pseudorabdion collaris*
    - *longiceps*
  - *Stilostoma extenuatum*
- Elapidae
  - *Elaps lacteus*
  - *Leptomicrurus collaris*
  - *Ogmodon vitianus*
  - *Parapistocalamus hedgeri*
  - *Ultrocalamus preussi*

Intraspecific variation between States I and III is reported by G. A. Boulenger (1894, 1896) in *Erythrolamprus decipiens* and *Aparallactus nigriceps.*

In the above colubrids this character state has a higher frequency of correlation with derived states of 14 other characters compared to the frequency distribution of these states of the same 14 characters in the total sample (table 21) (Criterion 3). These colubrids are all confined to the fossorial habitat (table 22) (Criterion 5). Also 7 of these 11 species are members of the calamarine group (Inger and Marx, 1965, table 58) (Criterion 7). The application of the four criteria (2, 3, 5, 7) indicates that State III is derived (Criterion 8).

Character State II is rare in the colubrids (table 20).

State II, many anterior temporals, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Boiga kraepelini*
  - *Chionactis occipitalis*
  - *Elaphe subocularis*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Homalopsis buccata*
  - *Pythonodipsas carinatus*
  - *Scaphiophis albopunctatus*
  - *Spalerosophis diadema*
- Hydrophiidae
  - *Kolpophis annandalei*

Viperinae
*Atheris*
*Bitis*
*Cerastes*
*Echis*
*Eristicophis*
*Vipera*

Crotalinae
*Agkistrodon contortrix*
*hypnale*
*nepa*
*piscivorus*
*Bothrops*
*Crotalus*
*Lachesis*
*Sistrurus*
*Trimeresurus*

Intraspecific variation occurs in *Aipysurus laevis* (M. A. Smith, 1926).

In the above colubrids this character state has a higher frequency of correlation with derived states of 10 other characters compared to the frequency distribution of these states of the same 10 characters in the total sample (table 21) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the terrestrial habitat (60.0 per cent) compared to the relative abundance of terrestrial colubrid species in the total sample (36.2 per cent) (table 22) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

TABLE 21. Correlation of States II and III of Character 9 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 9 | In species having State III of Character 9 | In total working sample |
| 1 | 70.0% (5)* | 63.6% (3) | 14.3% (28) |
| 2 | 40.0 (2) | | 15.6 (31) |
| 5 | | 36.4 (3) | 3.5 (9) |
| 7 | | 100.0 (6) | 25.5 (56) |
| 11 | 60.0 (6) | 72.7 (3) | 26.7 (50) |
| 12 | 80.0 (8) | | 4.8 (13) |
| 13 | | 54.5 (3) | 31.8 (54) |
| 14 | 50.0 (3) | | 3.5 (7) |
| 16 | 70.0 (5) | | 21.7 (34) |
| 17 | 70.0 (5) | | 35.4 (48) |
| 19 | | 100.0 (6) | 36.8 (68) |
| 22 | | 36.4 (2) | 4.5 (11) |
| 25 | | 50.0 (2) | 6.3 (12) |
| 28 | | 63.6 (4) | 11.7 (26) |
| 29 | | 33.3 (3) | 10.1 (27) |
| 31 | 44.4 (4) | 44.4 (4) | 19.5 (44) |
| 32 | | 100.0 (6) | 26.3 (55) |
| 33 | 70.0 (5) | | 43.0 (76) |
| 40 | 66.7 (4) | 55.6 (4) | 24.8 (54) |
| 50 | | 77.8 (4) | 20.0 (24) |

* Number of genera.

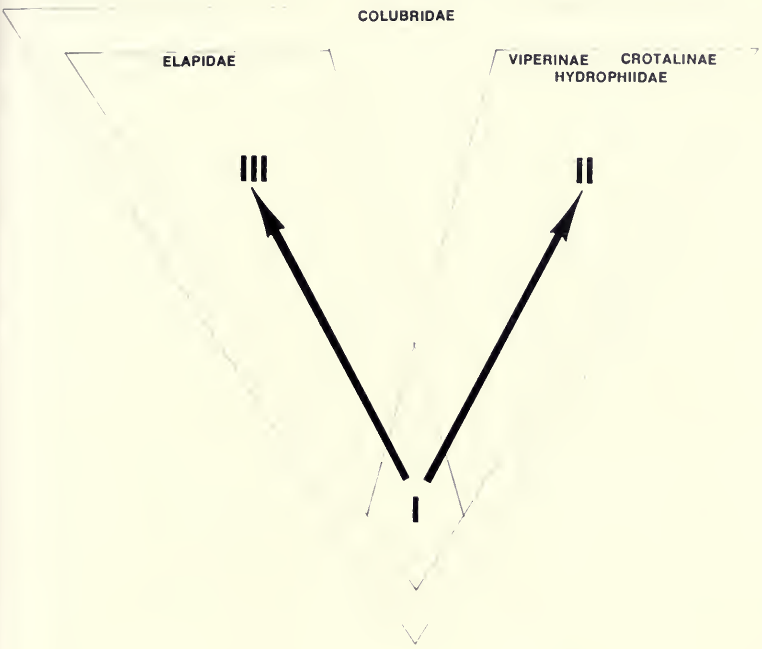

FIG. 9. Distribution among families of states of Character 9. Direction of change among states shown by arrows.

From the numerical order it appears that States II and III represent change in different directions from State I. In support, there is intraspecific variation between States I and II, as well as I and III, but no intraspecific variation between States II and III. Each derived state is overwhelmingly abundant in different families (table 20) and among taxa of different habitat zones (table 22).

One or two temporals are most abundant in the colubrid taxa (table 23). One anterior temporal is more abundant in secretive taxa (fossorial and subterrestrial) than more than one temporal (table 22). Few or no temporals have long been considered characteristic of fossorial snakes (e.g., Inger and Marx, 1965, table 58). However, species with one anterior temporal are fairly evenly distributed in all the habitat zones in our working sample (table 22).

In the true viper *Adenorhinos* the presence of a single temporal appears to us as a derived condition (a reversal within the family). *Adenorhinos* has a shortened head and, as implied by Marx and Rabb (1965), this modification may be an adjustment to eating soft prey. This kind of modification appears in unrelated slug-eating snakes

TABLE 22. Habitat distribution of colubrid species having States I, II, and III of Character 9 compared to the total colubrid working sample.

| Description | Total working Sample | STATES | | | |
|---|---|---|---|---|---|
| | | I | II | | III |
| Temporals | | One | Two-Three | 3 plus | Absent |
| Terrestrial | 36.2% | 23.7% | 49.2% | 60.0% | |
| Arboreal | 16.5 | 17.3 | 16.9 | 10.0 | |
| Aquatic | 14.9 | 21.6 | 10.8 | 10.0 | |
| Subterrestrial | 10.8 | 19.4 | 4.6 | | |
| Fossorial | 12.4 | 12.2 | 3.1 | 20.0 | 100.0% |
| Variation | 5.7 | 2.2 | 11.5 | | |
| Unknown | 3.5 | 3.6 | 3.8 | | |

(*ibid*, fig. 41A—B). See Character 7 for further discussion on consolidation of head shields in this genus.

Our interpretation of the phyletics of Character 9 is shown in Figure 9.

## Character 10—Interoculabials

### DESCRIPTION OF CHARACTER

The interoculabials are here defined as the scale rows between the suboculars (Character 12) and the supralabials (Character 11). This is a modification of the definition given by Klauber (1956, p. 95), for he included the suboculars and supralabials, i.e., scale rows between eye and lip. Analysis is confined to the presence or absence of interoculabials, i.e., the separation of the supralabials from the oculars.

Three states are recognized:

State I —interoculabials absent
State II —intraspecific variation, both States I and III present
State III—interoculabials present

### FAMILIAL RANGES OF VARIATION (Table 24)

Colubridae, Elapidae, Hydrophiidae—All taxa in these three familial groups have State I in a sample of 533 species (400, 91, 42 respectively) of 278 genera (220, 42, 16).

M. A. Smith (1943, fig. 123) illustrated intervening scales between the supralabials and suboculars in *Homalopsis buccata* and

TABLE 23. Distribution of relative abundance of the number of anterior temporals.

| Family<br>Species (Genera) | Colubridae[1]<br>990 (198)[5] | Elapidae[1]<br>132 (29) | Hydrophiidae[2]<br>47 (15) | Viperinae[3]<br>35 (8) | Crotalinae[3]<br>45 (6) | *Azemiops*[3]<br>1 | *Atractaspis*[4]<br>14 (1) |
|---|---|---|---|---|---|---|---|
| Number of Anterior Temporals | | | | | | | |
| 0 | 8.5% | 1.5% | | | | | |
| 0–1[6] | 0.2 | | | | | | |
| 1 | 50.0 | 57.6 | 34.0% | 2.9% | 4.4% | | 71.4% |
| 1–2 | 11.3 | 1.5 | 8.5 | | | | |
| 2 | 23.2 | 36.4 | 21.3 | 17.1 | | 100.0% | 14.3 |
| 1–3 | 0.2 | | 2.1 | | | | |
| 2–3 | 3.8 | 3.0 | 25.5 | | 6.7 | | |
| 2–4 | | | 2.1 | | | | |
| 3 | 1.4 | | 4.3 | | | | 14.3 |
| 3+ | 1.3 | | 2.1 | 80.0 | 88.9 | | |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

[5] Number of genera.

[6] Intraspecific variation.

TABLE 24. Distribution of character states of the interoculabials.

| | | STATES | | | |
|---|---|---|---|---|---|
| | | I | II | III | |
| Description | | Absent | Intraspecific Variation | Present | |
| | | | SPECIES | | |
| Colubridae[1] | —400 | 100.0% | | | |
| Elapidae[1] | — 91 | 100.0 | | | |
| Hydrophiidae[2] | — 42 | 100.0 | | | |
| Viperinae[3] | — 38 | 34.2 | 7.9% | 57.9% | |
| Crotalinae[3] | — 45 | 37.8 | 4.4 | 57.8 | |
| *Azemiops*[3] | — 1 | 100.0 | | | |
| *Atractaspis*[4] | — 16 | 100.0 | | | |
| | | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | —220 | 100.0 | | | |
| Elapidae | — 42 | 100.0 | | | |
| Hydrophiidae | — 16 | 100.0 | | | |
| Viperinae | — 8 | 25.0 | | 50.0 | 25.0% |
| Crotalinae | — 6 | 33.3 | | 16.7 | 50.0 |
| *Azemiops* | — 1 | 100.0 | | | |
| *Atractaspis* | — 1 | 100.0 | | | |

[1] Suite of references.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

stated in text that "often 2–3 suboculars separating eye from the labials." Specimens we have examined (FMNH: 10 species from Thailand, Cochinchina, Malaya, and Java) have some supralabials touching the eye in some specimens, others have suboculars but none have intervening scales between the suboculars and supralabials.

Viperinae—The true vipers have all three states in a sample of 38 species of the 8 genera. State I occurs in 13 species of 4 genera, II in 3 species of 2 genera, III in 22 species of 6 genera.

Intrageneric variation occurs in *Vipera* and *Atheris.*

Crotalinae—The pit-vipers have all three states in a sample of 45 species of the 6 genera. State I occurs in 17 species of 4 genera, II in 2 species of *Trimeresurus,* III in 26 species of 4 genera.

Intrageneric variation occurs in *Bothrops, Crotalus* (I, II), and *Trimeresurus* (I, II, III).

*Azemiops* and *Atractaspis* have State I.

### PHYLETICS OF CHARACTER 10

States II and III do not occur in the colubrids (table 24). We apply the uniqueness criterion (1) and the closely related taxa criterion (7) to character states II and III since they are unique to a derived stock, the Viperidae.

By definition, State II is an intermediate state.

Many viperid taxa have interoculabials (III) and some species show intraspecific variation (II).

These taxa are:

- State II
  - Viperinae
    - *Vipera aspis*
      - *xanthina*
    - *Atheris squamiger*
  - Crotalinae
    - *Trimeresurus flavoviridis*
      - *wagleri*
- State III
  - Viperinae
    - *Vipera ammodystes*
      - *latasti*
      - *lebetina*
      - *persica*
      - *russelii*
    - *Atheris chlorechis*
      - *nitschei*
    - *Bitis*
    - *Cerastes*
    - *Echis*
    - *Eristicophis*
  - Crotalinae
    - *Bothrops alternatus*
      - *atrox*
      - *barnetti*
      - *dunni*
      - *godmani*
      - *jararacussu*
      - *lansbergii*
      - *neuwiedi*
      - *nummifer*
      - *schlegeli*
    - *Trimeresurus monticola*
      - *mucrosquamatus*
      - *okinavensis*
      - *puniceus*
    - *Crotalus*
    - *Lachesis*

Interoculabials are present in the viperines in species of all modes of life (fossorial, terrestrial, and arboreal), climates, ranges, etc. and, therefore, we believe this state has no adaptive advantage in relation to environmental conditions. The fragmentation of scales in the suborbital region of the heads of advanced vipers is associated with

TABLE 25. Range of interoculabial rows in Viperinae, *Azemiops*, and *Atractaspis*.

| | Interoculabial rows | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 0 | 0–1 | 1 | 1–2 | 2 | 2–3 | 2–4 | 3 | 3–4 |
| *Atractaspis* | 16 | | | | | | | | |
| *Azemiops* | 1 | | | | | | | | |
| *Causus* | 6 | | | | | | | | |
| *Vipera* | 3 | 2 | 2 | 1 | | 2 | | | |
| *Eristicophis* | | | | | | | | 1 | |
| *Echis* | | | 1 | | | 1 | | | |
| *Cerastes* | | | | | | | | 1 | 1 |
| *Atheris* | 3 | 1 | 2 | 1 | | | | | |
| *Bitis* | | | 1 | | 2 | 3 | 1 | 1 | |
| *Adenorhinos* | 1 | | | | | | | | |

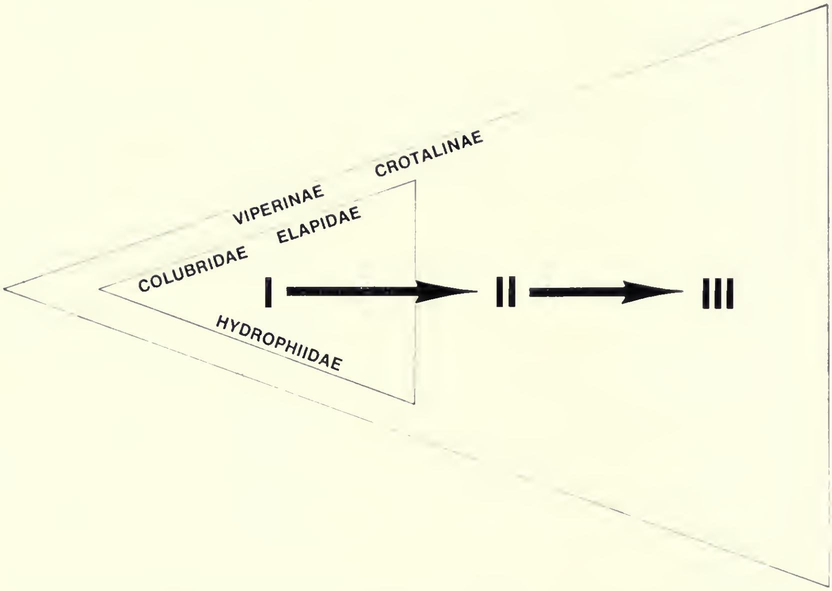

Fig. 10. Distribution among families of states of Character 10. Direction of change among states shown by arrows.

fragmentation of other head scales. The fragmentation of these head shields probably facilitates movement in the cranial area for erection of maxillary apparatus.

There are differences in the number of interoculabial rows among the true vipers (table 25). Probably the greater numbers of interoculabial rows are more derived conditions. However, we do not see any distinct breaking point in this series and therefore we have grouped all species with interoculabials into a single state (III).

Our interpretation of the phyletics of Character 10 is shown in Figure 10.

## Character 11—Number of Supralabials

### Description of Character

Supralabials are the shields that form the upper lip of the mouth. They are counted on one side of the head from the rostral shield (mid-shield on snout) posteriorly to the final shield that can be lifted to see the inside of the mouth. See Peters (1964, p. 180) for a description of labials.

TABLE 26. Spans in number of supralabials by species and families.

| Span | All families | Number of Species<br>Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3,4] | Crotalinae[3] |
|---|---|---|---|---|---|---|
| 1 | 1,018 | 867 | 128 | 16 | 5 | 2 |
| 2 | 156 | 103 | 8 | 24 | 6 | 15 |
| 3 | 41 | 12 |  | 10 | 8 | 11 |
| 4 | 15 | 1 |  |  | 10 | 4 |
| 5 | 8 | 1 |  |  | 7 |  |
| 6 | 8 |  |  |  | 1 | 7 |
| 7 | 1 |  |  |  |  | 1 |
| 8 | 4 |  |  |  |  | 4 |
| 10 | 1 |  |  |  |  | 1 |
| Totals | 1,252 | 984 | 136 | 50 | 37 | 45 |
| Span 3 or less | 97.0% | 99.8% | 100.0% | 100.0% | 51.4% | 62.2% |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Excluding *Azemiops* and *Atractaspis*.

TABLE 27. Distribution of character states of the number of supralabials.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Classes[1] | 3 | 4–5 | 6–9 | 1–2 |
| | | SPECIES | | |
| Colubridae —984 | 73.3% | 18.8% | 0.6% | 7.3% |
| Elapidae —136 | 98.5 | | | 1.5 |
| Hydrophiidae— 50 | 84.0 | 8.0 | | 8.0 |
| Viperinae — 37 | 18.9 | 40.5 | 37.8 | 2.7 |
| Crotalinae — 45 | 31.1 | 40.0 | 28.9 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 15[2] | 33.3 | | | 66.7 |
| | | GENERA | | |
| Colubridae —199 | 71.9 | 19.2 | 1.5 | 7.5 |
| Elapidae — 29 | 93.1 | | | 6.9 |
| Hydrophiidae— 16 | 75.0 | 18.8 | | 6.3 |
| Viperinae — 8 | 12.5 | 25.0 | 50.0 | 12.5 |
| Crotalinae — 6 | 16.7 | 50.0 | 33.3 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | | | 100.0 | |

[1] See Table 26.

[2] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

## Ranges as Data

Four meristic characters used in this study (scale rows at midbody, supralabials, ventrals, and subcaudals) only have ranges given for each species (literature cited in tables 26 and 27). Our method of assigning species and genera to a class (table 28) is as follows: non-overlapping classes are established (e.g., Class I = 1 to 10 and Class III = 11 to 20). If a given taxon falls into one of these classes by at least two-thirds of its range (example: range 4 to 13, span of 10—7 in Class I and 3 in Class III), it is assigned to that class. If the range does not fall into a non-overlapping class by two-thirds or more, it is assigned to an intermediate class (i.e., range of 7–13 is assigned to Class II).

The advantage of this method of handling meristic states is that it allows for the entire species and generic range and avoids partitioning of data due to sexual dimorphism. In many cases the species sample is inadequate to give little more than an indication of mean, median, or sexual dimorphism. However, almost certainly in the vast majority of cases if two-thirds of a range falls into a class, the mean and median also will fall into the same class.

States were established at marked changes in frequency of species between classes.

TABLE 28. Frequency distribution of species in range classes of number of supralabials in families of advanced snakes.

| Class | Range | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 3–5 | 69/14 | 1/0 | 2/1 | | |
| 2 | Intermediate[2] | 3/1 | 1/2 | 2/0 | 1/1 | |
| 3 | 6–8 | 721/143 | 134/27 | 42/12 | 7/1 | 14/1 |
| 4 | Intermediate | 50/21 | | 1/1 | 3/0 | 6/1 |
| 5 | 9–11 | 135/17 | | 3/2 | 12/2 | 12/2 |
| 6 | Intermediate | 1/1 | | | 3/0 | 1/1 |
| 7 | 12–14 | 3/2 | | | 7/2 | 4/0 |
| 8 | Intermediate | 1/0 | | | 2/1 | 3/1 |
| 9 | 15–17 | 1/0 | | | 2/1 | 5/0 |
| Totals | | 984/199 | 136/29 | 50/16 | 37/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] See text for explanation.

## CLASSES AND STATES

The total range of variation in number of supralabials was segmented by steps of three, since a span of three covered most of the intraspecific variation encountered (97.0 per cent—table 26). Using ranges as data, nine classes resulted, as shown in Table 28.

Four states are recognized:

State I —Class 3 (6–8 supralabials)
State II —Classes 4–5 (*c.* 8–11)
State III—Classes 6–9 (*c.* 11–17)
State IV—Classes 1–2 (3–*c.*6)

## FAMILIAL RANGES OF VARIATION (Table 27)

Colubridae—This family has all four states in a sample of 984 species of 199 genera. State I occurs in 721 species and 143 genera, II in 185 species and 38 genera, III in 6 species and 3 genera, and IV in 72 species and 15 genera.

The range of supralabials is from 4 (*Amblyodipsas microphthalama, Tetralepis fruhstorferi,* 10 species of *Calamaria*) to 15 (*Herpeton tentaculatum, Hypsirhina doriae, Spalerosophis microlepis*). The maximum span is 5 (*Spalerosophis diadema*).

Elapidae—This family has States I and IV in a sample of 136 species of 29 genera. State I occurs in 134 species of 27 genera; IV in 2 species of 2 genera.

The range of supralabials is from 5 (*Furina bimaculata, Rhynchoelaps semifasciata*) to 8 (4 species of *Dendroaspis*). The maximum span is 2 (8 species of 4 genera).

Hydrophiidae—The sea snakes have States I, II, and IV in a sample of 50 species of the 16 genera. State I occurs in 42 species and 12 genera; II in 4 species and 3 genera; IV in 4 species and 1 genus.

The range of supralabials is from 3 (2 species of *Emydocephalus*) to 11 (*Kolpophis annandalei*). The maximum span is 3 (10 species of 5 genera).

Viperinae—The true vipers have all four states in a sample of 37 species of the 8 genera. State I occurs in 7 species and 1 genus; II in 15 species and 2 genera; III in 14 species and 4 genera. State IV occurs in monotypic *Adenorhinos.*

The range of supralabials is from 5 (*Adenorhinos barbouri*) to 18 (*Bitis nasicornis*). The maximum span is 6 (*Atheris squamiger*).

Crotalinae—The pit vipers have States I, II, and III in a sample of 45 species of the 6 genera. State I occurs in 14 species and 1 genus; II in 18 species and 3 genera; III in 13 species and 2 genera.

The range of supralabials is from 6 (*Agkistrodon strauchi*) to 20 (*Crotalus molossus*). The maximum span is 10 (*Crotalus viridis*).

*Azemiops* has State I.

*Atractaspis* has States I and IV. The range is from 5 (9 species) to 7 (*A. scortecci*). All species have a span of 1.

## PHYLETICS OF CHARACTER 11

A substantial majority of the colubrids exhibit character State I, having 6–8 supralabials. Character State II is not particularly rare in the colubrids (table 27). It occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Boiga blandingi*
  - *cynodon*
  - *dendrophilia*
  - *irregularis*
  - *kraepelini*
  - *pulverulentus*
- *Chironius carinatus*
  - *fuscus*
- *Chrysopelea ornata*
- *Coluber florulentus*
  - *hippocrepis*
  - *najadum*
  - *rhodorhachis*
  - *rogersi*
  - *spinalis*
  - *ventromaculatus*
- *Crotaphopeltis hotamboeia*
- *Cyclagras gigas*
- *Dipsadoboa unicolor*
- *Dromophis lineatus*
- *Dryadophis amarali*
  - *boddaerti*
- *Drymobius margaritiferus*
- *Dugandia bicincta*
- *Elaphe dione*
  - *flavirufa*
  - *frenatus*
  - *guttata*
  - *radiata*
  - *subocularis*
  - *taeniura*
- *Gastropyxis smaragdina*
- *Gonyosoma oxycephalum*
- *Hapsidophrys lineata*
- *Helicops leopardinus*
  - *schistosus*
- *Homalopsis buccata*
- *Hydraethiops melanogaster*
- *Hydrodynastes gigas*
- *Leptophis occidentalis*
- *Lycodon aulicus*
- *Malpolon monspessulanus*
- *Natrix aequifasciata*
  - *annularis*
  - *anoscopus*
  - *craspedogaster*
  - *percarinata*
  - *piscator*
  - *trianguligera*
- *Oxybelis aeneus*
  - *fulgidus*
- *Passerita mycterizans*
  - *prasinus*
- *Philothalmus heterodermus*
  - *irregularis*
- *Psammophis sibilans*
  - *subtaeniatus*
- *Pythonodipsas carinata*

- *Salvadora hexalepsis*
  - *lemniscata*
  - *mexicana*
- *Scaphiodontophis annulatus*
- *Siphlophis cervinus*
- *Stegonotus borneensis*
- *Telescopus semiannulatus*
- *Thamnophis eques*
  - *macrostemna*
- *Thelotornis kirtlandi*

Hydrophiidae
- *Aipysurus duboisii*
  - *laevis*
- *Astrotia*
- *Kolpophis*

Viperinae
- *Atheris hindii*
  - *nitschei*
  - *squamiger*
  - *superciliaris*
- *Cerastes vipera*
- *Echis carinatus*
- *Vipera ammodytes*
  - *berus*
  - *latasti*
  - *lebetina*
  - *russelii*
  - *xanthina*

Crotalinae
- *Agkistrodon contortrix*
- *Bothrops alternatus*
  - *cotiara*
  - *dunni*
  - *godmani*
  - *lansbergi*
  - *neuwiedi*
  - *nummifer*
  - *schlegeli*
- *Lachesis*
- *Sistrurus miliarius*
- *Trimeresurus albolabris*
  - *flavoviridis*
  - *monticola*
  - *mucrosquamatus*
  - *puniceus*
  - *stejnegeri*
  - *sumatranus*
  - *wagleri*

In the colubrids character State II has a higher frequency of correlation with derived states of four other characters compared to the frequency distribution of these states of the same four characters in the total sample (table 29) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the arboreal and aquatic habitats (47.1 per cent) compared to the relative abundance of arboreal and aquatic species in the total sample (31.4 per cent—table 30) (Criterion 5).

The application of two criteria (3, 5) suggests that this state is derived (Criterion 8).

Character State III is extremely rare in the colubrids (table 27) (Criterion 2) and is accordingly considered derived. State III, the maximum number of supralabials, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Opisthotropis kuatunensis*
- *Spalerosophis diadema*

Viperinae
- *Atheris chlorechis*
- *Bitis*
- *Cerastes cerastes*
- *Echis coloratus*
- *Eristicophis*
- *Vipera aspis*
  - *persica*

Crotalinae
*Crotalus*
*Sistrurus catenatus*

The serial nature of supralabials makes a single trend in the arrangement of States I, II, III most probable (fig. 11).

TABLE 29. Correlation of States II and IV of Character 11 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 11 | In species having State IV of Character 11 | In total working sample |
| 1 | | 75.0% (5) | 14.3% (28) |
| 4 | 10.3% (2)* | | 3.8 (4) |
| 5 | | 25.0 (2) | 3.5 (9) |
| 7 | | 83.3 (5) | 25.5 (56) |
| 9 | | 75.0 (4) | 6.8 (14) |
| 13 | 56.1 (20) | | 31.8 (54) |
| 16 | | 58.3 (3) | 21.7 (34) |
| 17 | 47.1 (17) | | 35.4 (48) |
| 19 | | 91.7 (6) | 36.8 (68) |
| 21 | 38.8 (12) | | 18.9 (29) |
| 22 | | 33.3 (2) | 4.5 (11) |
| 25 | | 37.5 (2) | 6.3 (12) |
| 28 | | 80.0 (5) | 11.7 (26) |
| 34 | | 42.9 (3) | 6.8 (18) |
| 36 | | 25.0 (3) | 6.1 (16) |
| 38 | | 71.4 (4) | 16.2 (27) |
| 39 | | 50.0 (3) | 9.0 (15) |
| 40 | | 45.5 (4) | 24.8 (54) |
| 47 | | 83.3 (6) | 48.5 (84) |
| 49 | | 30.0 (3) | 15.5 (26) |
| 50 | | 60.0 (3) | 20.0 (24) |

* Number of genera.

TABLE 30. Habitat distribution of colubrid species having States II and IV of Character 11 compared to the total colubrid working sample.

| | Total Working Sample | STATES | |
|---|---|---|---|
| | | II | IV |
| Terrestrial | 36.2% | 41.2% | |
| Arboreal | 16.5 | 25.0 | |
| Aquatic | 14.9 | 22.1 | |
| Subterrestrial | 10.8 | | 25.0% |
| Fossorial | 12.4 | 1.5 | 75.0 |
| Variation | 5.3 | 10.3 | |
| Unknown | 3.5 | | |

Character State IV is rare in the colubrids (table 27) (Criterion 2). State IV, a low number of supralabials, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *schlegeli*
    - *septentrionalis*
  - *Carphophis amoena*
  - *Chilorhinophis carpenteri*
  - *Haldea striatula*
  - *Pseudorabdion collaris*
    - *longiceps*
  - *Scaphiophis albopunctatus*
  - *Tropidocloniom lineatum*
- Elapidae
  - *Brachyurophis semifasciata*
  - *Toxicocalamus stanleyanus*
  - *Ultrocalamus preussi*
- Hydrophiidae
  - *Emydocephalus*
  - *Hydrophis brookii*
    - *klossi*
- Viperinae
  - *Adenorhinos barbouri*

- *Atractaspis corpulenta*
  - *dahomeyensis*
  - *irregularis*

In the colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total sample (table 29) (Criterion 3).

The colubrids exhibiting State IV are all species of secretive habits (subterrestrial and fossorial), whereas the relative abundance of secretive colubrid species in the total sample is only 23.2 per cent (Criterion 5).

The application of three criteria (2, 3, 5) strongly indicates that State IV is derived (Criterion 8).

State IV probably arose differently from State II because these states correlate with derived states of different characters (table 29) and preponderate in different habitat zones (table 30).

Our interpretation of the phyletics of Character 11 is shown in Figure 11.

## Character 12—Eye Position to Supralabials

### DESCRIPTION OF CHARACTER

The eye is either in contact with one or more supralabials or separated from the supralabials by one or more suboculars and/or interoculabials.

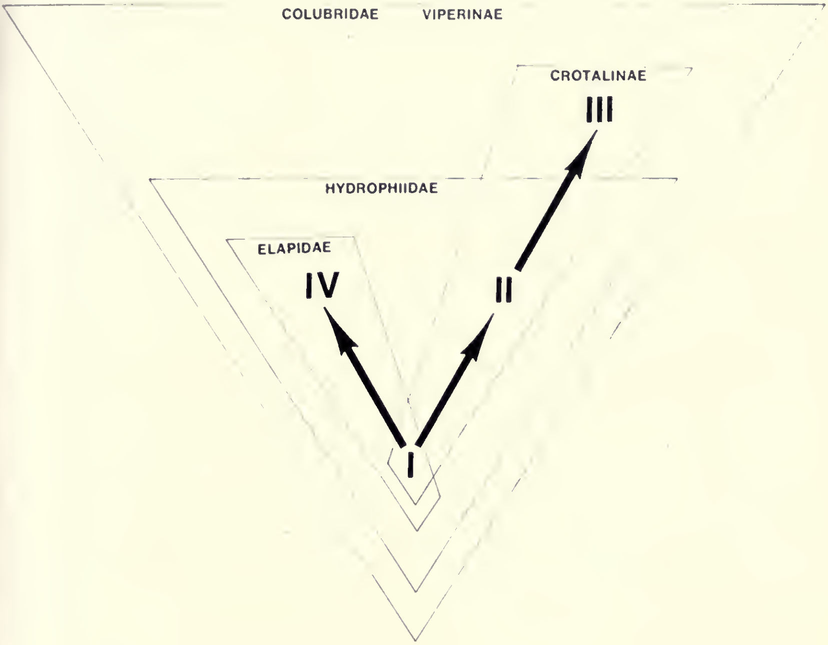

FIG. 11. Distribution among families of states of Character 11. Direction of change among states shown by arrows.

Three states are recognized:

State I —eye in contact with supralabials
State II —eye not in contact with supralabials
State III—intraspecific variation, both States I and II present

### FAMILIAL RANGES OF VARIATION (Table 31)

Colubridae—This family has all three states in a sample of 1,001 species of 199 genera. State I occurs in 965 species of 180 genera, II in 30 species of 11 genera, III in 6 species. Boulenger reported intrageneric variation in 8 genera.

Elapidae—This family has States I and II in a sample of 138 species of 29 genera. State I occurs in 136 species of 27 genera, II in 2 species of 2 genera. Intrageneric variation occurs in *Naja.*

Hydrophiidae—The sea-snakes have States I and III in a sample of 42 species of the 16 genera. State I occurs in 41 species of 15

TABLE 31. Distribution of character states of the suboculars.

| Description | | STATES I | STATES II | STATES III | |
|---|---|---|---|---|---|
| | | Eye in contact with supralabial | Eye separated from supralabials | Intraspecific variation | |
| | | | SPECIES | | |
| Colubridae[1] | —1,001 | 96.4% | 3.0% | 0.6% | |
| Elapidae[1] | — 138 | 98.6 | 1.4 | | |
| Hydrophiidae[2] | — 42 | 97.6 | | 2.4 | |
| Viperinae[3] | — 38 | | 100.0 | | |
| Crotalinae[3] | — 45 | 6.7 | 93.3 | | |
| *Azemiops*[3] | — 1 | 100.0 | | | |
| *Atractaspis*[4] | — 16 | 100.0 | | | |
| | | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | — 199 | 90.5 | 5.5 | | 4.0% |
| Elapidae | — 29 | 93.1 | 3.4 | | 3.4 |
| Hydrophiidae | — 16 | 93.8 | | | 6.3 |
| Viperinae | — 8 | | 100.0 | | |
| Crotalinae | — 6 | | 66.7 | | 33.3 |
| *Azemiops* | — 1 | 100.0 | | | |
| *Atractaspis* | — 1 | 100.0 | | | |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

genera. Intraspecific variation (State III) occurs in the monotypic *Kolpophis annandalei.*

Viperinae—The true vipers have only State II in a sample of 38 species of the 8 genera.

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 3 species of 2 genera, II in 42 species of 6 genera.

Intrageneric variation occurs in *Agkistrodon* and *Crotalus.*

*Azemiops* and *Atractaspis* have State I.

### Phyletics of Character 12

Character State II is rare in the colubrids (Criterion 2) (table 31).

State II, eye not in contact with supralabials, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Dugandia bicolor*
  - *Elaphe subocularis*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Hydrodynastes gigas*
  - *Natrix cyclopion*
  - *Phyllorhynchus decurtatus*
  - *Pythonodipsas carinatus*
  - *Scaphiophis albopunctatus*
  - *Spalerosophis diadema*
- Elapidae
  - *Acanthophis antarticus*
  - *Naja haje*
- Viperinae
  - all
- Crotalinae
  - *Agkistrodon acutus*
    - *bilineatus*
    - *contortrix*
    - *hypnale*
    - *nepa*
    - *piscivorus*
    - *rhodostoma*
  - *Bothrops*
  - *Crotalus* (10 of 11 species)
  - *Lachesis*
  - *Sistrurus*
  - *Trimeresurus*

In these colubrids this character state has a higher frequency of correlation with derived states of 11 other characters compared to the frequency distribution of these states of the same 11 characters in the total sample (table 32) (Criterion 3).

The application of two criteria (2, 3) suggests that this state is derived (Criterion 8).

State III is present in four colubrids and a sea-snake. They are:

*Homalopsis buccata*
*Lystrophis d'orbignyi*
*Opisthotropis kuatuenensis*
*Salvadora hexalepsis*
*Kolpophis annandalei*

TABLE 32. Correlation of State II of Character 12 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters: In species having State II of Character 12 | | Frequency of derived states in indicated characters: In total working sample | |
|---|---|---|---|---|
| 1 | 54.5% | (4)* | 14.3% | (28) |
| 2 | 45.5 | (3) | 15.6 | (31) |
| 9 | 63.6 | (5) | 6.8 | (14) |
| 11 | 54.5 | (6) | 26.7 | (50) |
| 14 | 36.4 | (2) | 3.5 | (7) |
| 16 | 63.6 | (5) | 21.7 | (34) |
| 17 | 72.7 | (6) | 35.4 | (48) |
| 19 | 72.7 | (6) | 36.8 | (68) |
| 33 | 63.6 | (5) | 43.0 | (76) |
| 38 | 44.4 | (2) | 16.2 | (27) |
| 48 | 44.4 | (3) | 6.2 | (11) |

* Number of genera.

State III is an intermediate sequential state by definition—each taxon with this state has both States I and II.

Our interpretation of the phyletics of Character 12 is shown in Figure 12.

## Character 13—Eye Size

### DESCRIPTION OF CHARACTER

The eye size was measured relative to the distance from eye to the end of the snout.

Four states of relative eye size are recognized:

State I —moderate–eye two-thirds to three-fourths its distance to snout (Marx and Rabb, 1965, figs. 41E and G)

State II —small–eye about one-third to one-half its distance to snout

State III—minute–eye is less than one-third its distance to snout (Laurent, 1950)

State IV—large–eye is equal to or greater than its distance to snout (Marx and Rabb, *op. cit.*, figs. 41A and C).

### FAMILIAL RANGES OF VARIATION (Table 33)

Colubridae—This family has all four states in a sample of 311 species of 163 genera. State I occurs in 212 species of 123 genera, II

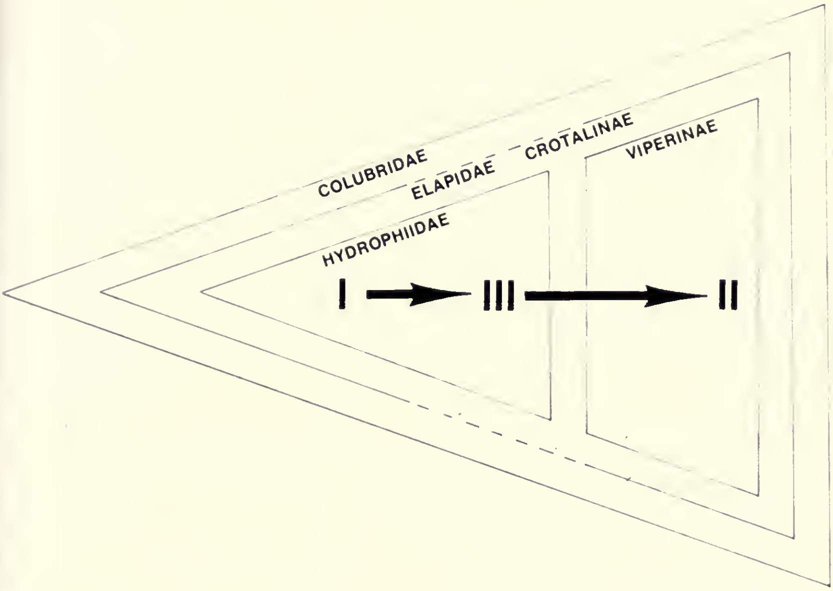

FIG. 12. Distribution among families of states of Character 12. Direction of change among states shown by arrows.

in 13 species of 11 genera, III in 3 species of 3 genera, IV in 83 species of 54 genera.

Intrageneric variation occurs in 6 genera; 5 with States I and IV, and 1 with States I, II, and IV.

Elapidae—This family has States I, II, and IV in a sample of 69 species of 38 genera. State I occurs in 45 species of 26 genera, II in 22 species of 11 genera, IV in 2 species of *Pseudohaje.*

Hydrophiidae—The sea-snakes have all four states in a sample of 42 species of the 16 genera. State I occurs in 38 species of 14 genera, II in two species of *Hydrophis,* III in monotypic *Hydrelaps,* IV in monotypic *Acalyptophis.* Intrageneric variation occurs in *Hydrophis* (I and II).

Viperinae—The true vipers have States I, II, and IV in a sample of 38 species of the 8 genera. State I occurs in 34 species of 6 genera, II in 3 species of 2 genera, IV in monotypic *Adenorhinos.*

Intrageneric variation occurs in *Bitis.*

Crotalinae—The pit vipers have States I and IV in a sample of 45 species of the 6 genera. State I occurs in 43 species of the 6 genera, IV in 2 species.

TABLE 33. Distribution of character states of the size of the eye.

| | STATES | | | | |
|---|---|---|---|---|---|
| Description | IV large | I moderate | II small | III minute | |
| | | SPECIES | | | |
| Colubridae —311[1] | 26.7% | 68.2% | 4.2% | 1.0% | |
| Elapidae — 69[1] | 2.9 | 65.2 | 31.9 | | |
| Hydrophiidae— 42[1] | 2.4 | 90.5 | 4.8 | 2.4 | |
| Viperinae — 38[1] | 2.6 | 89.5 | 7.9 | | |
| Crotalinae — 45[1] | 4.4 | 95.6 | | | |
| *Azemiops* — 1[1] | | 100.0 | | | |
| *Atractaspis* — 16[2] | | | | 100.0 | |
| | | GENERA | | | INTRAGENERIC VARIATION |
| Colubridae —163 | 22.1 | 67.5 | 4.9 | 1.8 | 3.7% |
| Elapidae — 38 | 2.6 | 68.4 | 28.9 | | |
| Hydrophiidae— 16 | 6.3 | 81.3 | | 6.3 | 6.3 |
| Viperinae — 8 | 12.5 | 62.5 | 12.5 | | 12.5 |
| Crotalinae — 6 | | 66.7 | | | 33.3 |
| *Azemiops* — 1 | | 100.0 | | | |
| *Atractaspis* — 1 | | | | 100.0 | |

[1] Working sample.

[2] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Intrageneric variation occurs in *Bothrops* and *Trimeresurus*. *Azemiops* has State I. *Atractaspis* has State III.

## PHYLETICS OF CHARACTER 13

Character State II is rare in the colubrids (Criterion 2) (table 33). State II, a small eye, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Achalinus spinalis*
- *Brachyorrhus albus*
- *Calamaria schlegeli*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Cyclocorus lineatus*
- *Geophis multitorques*
  - *semidoliatus*
- *Macrocalamus lateralis*
- *Miodon gabonensis*
- *Opisthotropis kuatuenensis*
  - *latouchi*
- *Prosymna ambigua*

Elapidae
- *Apistocalamus lonnbergi*
  - *loriae*
- *Bungarus candidus*
  - *fasciatus*
  - *multicinctus*
- *Elaps lacteus*
- *Glyphodon tristis*
- *Leptomicrurus collaris*
  - *narducci*
- *Micropechis elapsoides*
  - *ikaheka*
- *Micruroides euryxanthus*
- *Micrurus affinis*
  - *fulvius*

  *lemniscatus*
  *mipartitus*
  *nigrocinctus*
  sp.
  *spixi*
*Ogmodon vitianus*
*Parapistocalamus hedigeri*
*Ultrocalamus preussi*
Hydrophiidae
  *Hydrophis melanosoma*
    *mertoni*
Viperinae
  *Bitis peringueyi*
  *Cerastes cerastes*
    *vipera*

In these colubrids this character state has a higher frequency of correlation with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total sample (table 34) (Criterion 3).

TABLE 34. Correlation of States II and IV of Character 13 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 13 | In species having State IV of Character 13 | In total working sample |
| 1 | 46.2% (5)* | | 14.3% (28) |
| 2 | 30.8 (3) | | 15.6 (31) |
| 4 | | 12.0% (2) | 3.8 (4) |
| 7 | 84.6 (9) | | 25.5 (56) |
| 11 | | 48.8 (27) | 26.7 (50) |
| 19 | 75.0 (7) | | 36.8 (68) |
| 21 | | 34.1 (18) | 18.9 (29) |
| 22 | 38.5 (5) | | 4.5 (11) |
| 26 | | 21.2 (8) | 12.6 (19) |
| 28 | 50.0 (4) | | 11.7 (26) |
| 32 | 62.5 (4) | | 26.3 (55) |
| 36 | 38.5 (4) | | 6.1 (16) |
| 38 | 57.1 (4) | | 16.2 (27) |
| 44 | | 7.6 (3) | 4.5 (11) |

* Number of genera.

These colubrids also have a markedly larger number of species confined to the fossorial habitat (69.2 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (table 35) (Criterion 5).

The application of three criteria (2, 3, 5) strongly suggests that State II is derived (Criteria 8).

Character State III is very rare in the colubrids (Criterion 2) (table 33). State III, a minute eye, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Apostolepis ambinigra*
  - *Calamelaps unicolor*
  - *Elapomorphus blumii*
- Hydrophiidae
  - *Hydrelaps darwiniensis*

*Atractaspis*—all species

These minute-eyed colubrids (plus *Atractaspis*) are all secretive (one subterrestrial, all other fossorial), as are most species having small eyes (State II) (Criterion 5).

The application of two criteria suggests that State III is derived (Criterion 8). We believe that this state represents a second stage adaptation in eye size. We infer that the sequence of phyletic change was from State I through II to III, because there is a morphological gradient from moderate eye size through a smaller eye to finally a minute eye within the same adaptive type (burrowers).

Character State IV is not particularly rare in the colubrids (table 33). State IV, a large eye, occurs in the following 83 colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Aparallactus lunulatus*
    - *werneri*
  - *Arrhyton vittatum*
  - *Boiga blandingi*
    - *cynodon*
    - *dendrophila*
    - *irregularis*
    - *jaspidea*
    - *kraepelini*
    - *multimaculata*
    - *pulverulentus*
    - *trigonatus*
  - *Calamaria linnaei*
    - *pavimentata*
    - *septentrionalis*
  - *Chironius carinatus*
    - *fuscus*
  - *Chrysopelea ornata*
  - *Coluber florulentus*
    - *gemonensis*
    - *hippocrepis*
    - *jugularis*
    - *rhodorhachis*
    - *rogersi*
    - *spinalis*
    - *ventromaculatus*
  - *Crotaphopeltis hotamboeia*
  - *Cryophis hallbergi*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Dipsadoboa unicolor*
  - *Dispholidus typus*
  - *Dromicodryas bernieri*
  - *Dromophis lineatus*
    - *praeornata*
  - *Duberria lutrix*
  - *Elaphe subocularis*
  - *Gastropyxis smaragdina*
  - *Hapsidophrys lineata*
  - *Leptophis mexicanus*
    - *occidentalis*
  - *Limnophis bicolor*
  - *Liodytes alleni*
  - *Liopholidophis lateralis*
  - *Lycodon aulicus*
  - *Malpolon moilensis*
    - *monspessulanus*
  - *Mimophis mahfalensis*
  - *Natriciteres olivacea*
  - *Oxybelis aeneus*
    - *argenteus*
    - *brevirostris*
    - *fulgidus*

- *Passerita mycterizans*
  - *nasuta*
  - *prasinus*
- *Philothalmus heterodermus*
  - *irregularis*
- *Phyllorhynchus decurtatus*
- *Pituophis deppei*
  - *melanoleucus*
  - *sayi*
- *Psammophis sibilans*
  - *subtaeniatus*
- *Psammophylax rhombeatus*
- *Pseudoxenodon striaticaudatus*
- *Rhamnophis aethiopissa*
- *Salvadora bairdi*
  - *grahami*
  - *hexalepis*
  - *lemniscata*
  - *lineata*
  - *mexicana*
- *Sibon sibon*
- *Storeria dekayi*
  - *occipitomaculata*
- *Telescopus iberus*
  - *semiannulatus*
- *Thelotornis kirtlandi*
- *Thrasops flavigularis*
- *Zaocys dhumnades*
  - *nigromarginatus*

Elapidae
- *Pseudohaje goldii*
  - *nigra*

Hydrophiidae
- *Acalyptophis peronii*

Viperinae
- *Adenorhinos barbouri*

Crotalinae
- *Bothrops alternatus*
- *Trimeresurus wagleri*

In these colubrids this character state has a higher frequency of correlation with derived states of five other characters compared to the frequency distribution of these states of the same five characters in our total sample (table 34) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the arboreal habitat (37.3 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent) (table 35) (Criterion 5).

The application of two criteria (3, 5) suggests that this character state is derived (Criterion 8).

We believe that the large-eyed state did not come from smaller or minute-eyed derived states because these states are associated

TABLE 35. Habitat distribution of colubrid species having States II and IV of Character 13 compared to the total colubrid working sample.

| | | STATES | |
|---|---|---|---|
| | Total working sample | II | IV |
| Terrestrial | 36.2% | | 30.1% |
| Arboreal | 16.5 | | 37.3 |
| Aquatic | 14.9 | 15.4% | 4.8 |
| Subterrestrial | 10.8 | 15.4 | 6.0 |
| Fossorial | 12.4 | 69.2 | 7.2 |
| Variation | 5.3 | | 14.5 |
| Unknown | 3.5 | | |

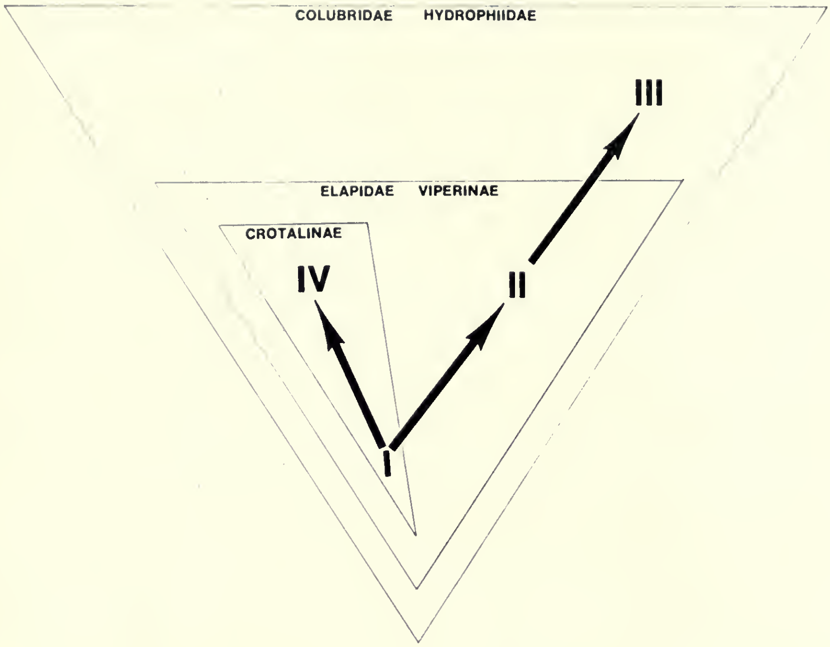

FIG. 13. Distribution among families of states of Character 13. Direction of change among states shown by arrows.

with sets of derived states of different characters, and, further, that these different eye sizes are primarily found in snakes occupying different habitat zones.

Our interpretation of the phyletics of character 13 is shown in Figure 13.

### Character 14—Mid-Throat Scalation

#### DESCRIPTION OF CHARACTER

The gular scales are relatively small scales of the chin or throat. They are surrounded by the infralabials, chin shields, and anterior ventral plates (Peters, 1964, p. 143). The chin shields are the scales dividing the gulars along the midline on the underside of the head. In some forms the posterior chin shields are either reduced in size or are replaced by gulars.

Two states are recognized:

State I —Midline is occupied by larger chin shields (Marx and Rabb, 1965, fig. 41D, H)

TABLE 36. Distribution of character states of the abundance of gulars.

| Description | STATES<br>I<br>Few Gulars | <br>II<br>Numerous Gulars | |
|---|---|---|---|
| | SPECIES | | |
| Colubridae —225[1] | 96.4% | 3.6% | |
| Elapidae — 63[1] | 100.0 | | |
| Hydrophiidae— 42[2] | 76.2 | 23.8 | |
| Viperinae — 38[4] | 63.2 | 36.8 | |
| Crotalinae — 44[4] | 68.2 | 31.8 | |
| *Azemiops* — 1[4] | 100.0 | | |
| *Atractaspis* — 13[3] | | 100.0 | |
| | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —163 | 96.3 | 2.5 | 1.2% |
| Elapidae — 34 | 100.0 | | |
| Hydrophiidae— 16 | 68.8 | 25.0 | 6.3 |
| Viperinae — 8 | 50.0 | | 50.0 |
| Crotalinae — 6 | 50.0 | | 50.0 |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | | 100.0 | |

[1] Suite of References.

[2] M. A. Smith, 1926, 1931.

[3] Laurent, 1950.

[4] Working sample.

State II —Midline is occupied by numerous gular scales (*ibid.*, fig. 41F)

## FAMILIAL RANGES OF VARIATION (Table 36)

Colubridae—This family has States I and II in a sample of 225 species of 163 genera. State I occurs in 217 species of 157 genera, II in 8 species of 4 genera. Intrageneric variation occurs in 2 genera.

Elapidae—All taxa in this family have State I; sample of 63 species, 34 genera.

Hydrophiidae—Sea-snakes have States I and II in a sample of 42 species of the 16 genera. State I occurs in 32 species of 12 genera, II in 14 species of 5 genera. Intrageneric variation occurs in *Hydrophis*.

Viperinae—The true vipers have States I and II in a sample of 38 species in the 8 genera. State I occurs in 20 species of 6 genera, II in 14 species of 6 genera. Intrageneric variation occurs in 4 genera.

TABLE 37. Correlation of State II of Character 14 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State II of Character 14 | In total working sample |
| 1 | 54.5% (4)* | 14.3% (28) |
| 2 | 54.5 (3) | 15.6 (31) |
| 9 | 45.5 (3) | 6.8 (14) |
| 12 | 45.5 (3) | 4.8 (13) |
| 16 | 72.7 (5) | 21.7 (34) |
| 32 | 50.0 (3) | 26.3 (55) |
| 40 | 72.7 (5) | 24.8 (54) |

* Number of genera.

Crotalinae—The pit vipers have States I and II in a sample of 44 species of the 6 genera. State I occurs in 30 species of the 6 genera, II in 14 species of 3 genera. Intrageneric variation occurs in 3 genera.

*Azemiops* has State I. *Atractaspis* has State II.

## PHYLETICS OF CHARACTER 14

Character State II is rare in the colubrids (Criterion 2) (table 36). State II, numerous gulars, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Carphophis amoena*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Heterodon nasicus*
  - *platyrhinos*
  - *simus*
- *Homalopsis buccata*
- *Rhynchocalamus melanocephalus*
- *Scaphiophis albopunctatus*
- *Sonora episcopa*
  - *semiannulata*

Hydrophiidae
- *Astrotia stokesii*
- *Hydrophis caerulescens*
  - *cyanocinctus*
  - *inornatus*
  - *major*
  - *ornatus*
- *Kolpophis annandalei*
- *Lapemis curtus*
  - *hardwickii*
- *Pelamis platurus*

Viperinae
- *Atheris chlorechis*
  - *superciliaris*
- *Bitis:* all but *B. worthingtoni*
- *Cerastes cerastes*
  - *vipera*
- *Echis coloratus*
- *Eristicophis macmahoni*
- *Vipera persica*

*Atractaspis*

Crotalinae
- *Bothrops alternatus*
  - *atrox*
  - *barnetti*
- *Crotalus atrox*
  - *lepidus*

*mitchellei*
*molossus*
*ruber*
*viridis*

*Trimeresurus albolabris*
*monticola*
*mucrosquamatus*
*puniceus*
*stejnegeri*

In these colubrids this character state has a higher frequency of correlation with derived states of seven other characters compared to the frequency distribution of these states of the same seven characters in the total sample (table 37) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—63.6 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (Criterion 5). Also nine of these 11 colubrids are confined to North America (Criterion 6). The application of four criteria (2, 3, 5, 6) strongly suggests that State II is derived (Criterion 8).

Our interpretation of the phyletics of Character 14 is shown in Figure 14.

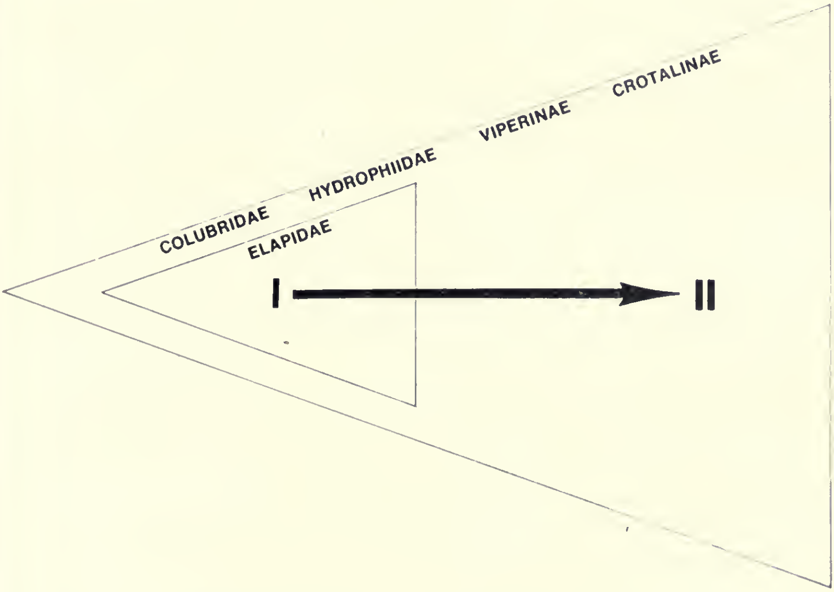

FIG. 14. Distribution among families of states of Character 14. Direction of change among states shown by arrows.

## Character 15—Carination of Gular Scales

### DESCRIPTION OF CHARACTER

The gulars are the small scales of the throat (Peters, 1964, p. 143).

Two states are recognized:

State I —gulars smooth (Marx and Rabb, 1965, fig. 41F)
State II —gulars keeled (*ibid.*, fig. 41H)

### FAMILIAL RANGES OF VARIATION (Table 38)

Colubridae, Elapidae, and Hydrophiidae—All taxa in these three familial groups have State I in a sample of 380 species (269, 69, 42 respectively) of 217 genera (167, 34, 16).

Viperinae—The true vipers have States I and II in a sample of 38 species of the 8 genera. State I occurs in 29 species of 6 genera, II in 9 species of 3 genera. Intrageneric variation occurs in *Atheris*.

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 44 species of the 6 gen-

TABLE 38. Distribution of character states of the gulars.

| | STATES | | |
|---|---|---|---|
| | I | II | |
| Description | Smooth | Keeled | |
| | SPECIES | | |
| Colubridae[1] —269 | 100.0% | | |
| Elapidae[1] — 69 | 100.0 | | |
| Hydrophiidae[2] — 42 | 100.0 | | |
| Viperinae[3] — 38 | 76.3 | 23.7% | |
| Crotalinae[3] — 45 | 97.8 | 2.2 | |
| *Azemiops*[3] — 1 | 100.0 | | |
| *Atractaspis*[4] — 13 | 100.0 | | |
| | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —167 | 100.0 | | |
| Elapidae — 34 | 100.0 | | |
| Hydrophiidae — 16 | 100.0 | | |
| Viperinae — 8 | 62.5 | 25.0 | 12.5% |
| Crotalinae — 6 | 83.3 | | 16.7 |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | 100.0 | | |

[1] Suite of References.
[2] M. A. Smith, 1926, 1931.
[3] Working sample.
[4] Laurent, 1950.

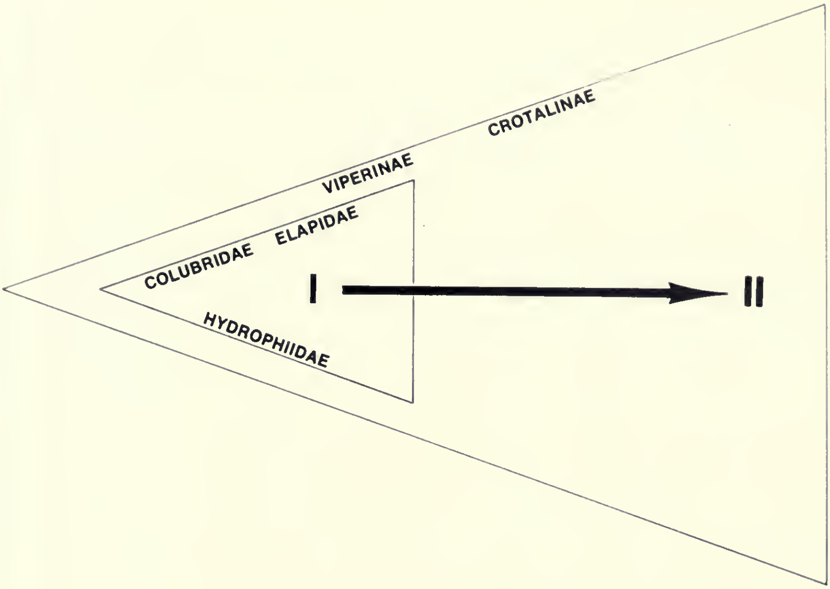

Fig. 15. Distribution among families of states of Character 15. Direction of change among states shown by arrows.

era, II only in *Trimeresurus wagleri*. Intrageneric variation thus occurs in *Trimeresurus*.

*Azemiops* and *Atractaspis* have State I.

### Phyletics of Character 15

State II, the presence of keels on the gular scales, does not occur in the colubrids and rarely occurs in a derived stock. We apply the uniqueness criterion (1) to character State II since its presence is unique to a derived stock.

Our interpretation of the phyletics of Character 15 is shown in Figure 15.

The taxa that have State II are:

Viperinae
  *Atheris ceratophorus*
    *chlorechis*
    *hispidus*
    *katangensis*
    *nitschei*
    *squamiger*
  *Cerastes cerastes*
    *vipera*
  *Eristicophis macmahoni*
Crotalinae
  *Trimeresurus wagleri*

Seven of the species are arboreal and the other three sand-sinkers.

## Character 16—Number of Scale Rows at Midbody

### DESCRIPTION OF CHARACTER

Body scales are arranged in longitudinal rows. The number of rows at midbody is the count we recorded. See Peters (1964, p. 311) for a description of this character.

### CLASSES AND STATES

The total range of variation in number of midbody scale rows was segmented by steps of four, since a span of four covered most of the intraspecific variation encountered (90.6 per cent—table 39).

TABLE 39. Spans in number of scale rows by species and families.

| | | Number of Species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3],[4] | Crotalinae[3] |
| 1 | 1031 | 881 | 122 | 8 | 6 | 14 |
| 3 | 117 | 85 | 10 | 6 | 7 | 9 |
| 4 | 3 | | | | 3 | |
| 5 | 47 | 23 | 4 | 7 | 7 | 6 |
| 6 | 2 | | | 1 | | 1 |
| 7 | 28 | 8 | | 4 | 5 | 11 |
| 8 | 3 | | | 1 | 2 | |
| 9 | 17 | 2 | 2 | 7 | 2 | 4 |
| 10 | 1 | | | 1 | | |
| 11 | 7 | 1 | | 4 | 2 | |
| 12 | 2 | | | | 2 | |
| 13 | 2 | | | 1 | 1 | |
| 14 | 3 | | | 3 | | |
| 15 | 1 | | | 1 | | |
| 16 | 1 | | | 1 | | |
| 17 | 1 | | | 1 | | |
| 18 | 1 | | | 1 | | |
| 19 | 1 | | | 1 | | |
| 20 | 1 | | | 1 | | |
| 27 | 1 | | | 1 | | |
| Totals | 1,270 | 1,000 | 138 | 50 | 37 | 45 |
| Span 4 or less | 90.6% | 98.9% | 95.7% | 28.0% | 43.2% | 51.1% |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Excluding *Azemiops* and *Atractaspis*.

The number of scale rows is one of four characters in this study for which only ranges were available in the literature for each taxon (table 39). Our method of using ranges as data is explained under Character 11. Twenty-two classes resulted, as shown in Table 40.

TABLE 40. Frequency distribution of species in range classes of number of scale rows in families of advanced snakes.

| | | Number of species/genera[1] | | | | |
|---|---|---|---|---|---|---|
| Class | Range | Colubridae | Elapidae | Hydrophiidae | Viperinae | Crotalinae |
| 1 | 10–13 | 87/6 | 18/2 | | | |
| 2 | 14–17 | 503/94 | 91/13 | 3/0 | 4/0 | 2/0 |
| 3 | Intermediate[2] | 0/5 | 2/4 | 0/1 | | |
| 4 | 18–21 | 276/60 | 16/5 | 7/1 | 6/1 | 7/0 |
| 5 | Intermediate | 2/8 | 4/1 | 1/3 | 4/1 | 5/1 |
| 6 | 22–25 | 82/10 | 7/3 | 4/0 | 6/1 | 16/1 |
| 7 | Intermediate | 7/7 | | 1/1 | 3/2 | 6/2 |
| 8 | 26–29 | 24/4 | | 1/1 | 5/0 | 4/1 |
| 9 | Intermediate | 6/2 | | | 3/2 | 2/0 |
| 10 | 30–33 | 8/0 | | | 2/1 | 1/0 |
| 11 | Intermediate | 1/1 | | 3/2 | 1/0 | 1/0 |
| 12 | 34–37 | 1/1 | | 2/0 | 1/0 | 1/1 |
| 13 | Intermediate | | | 3/0 | 2/0 | |
| 14 | 38–41 | 1/1 | | 7/1 | | |
| 15 | Intermediate | 1/1 | | 5/0 | | |
| 16 | 42–45 | 1/0 | | 3/2 | | |
| 17 | Intermediate | | | 2/0 | | |
| 18 | 46–49 | | | 3/0 | | |
| 19 | 50–53 | | | 1/0 | | |
| 20 | Intermediate | | | 1/1 | | |
| — | 54–57 | | | | | |
| 21 | Intermediate | | | 2/2 | | |
| — | 58–61 | | | | | |
| 22 | 82–85 | | | 1/1 | | |
| Totals | | 1,000/200 | 138/28 | 50/16 | 37/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] See Character 11 text for explanation.

Four states were recognized:

State I —Classes 2–4 (14–21 scale rows)
State II —Classes 5–8 (*c.* 21–29)
State III—Classes 9–22 (*c.* 29–85)
State IV—Class 1 (10–13)

## FAMILIAL RANGES OF VARIATION (TABLE 41)

Colubridae—This family has all four states in a sample of 1,000 species of 200 genera. State I occurs in 779 species and 159 genera, II in 115 species and 29 genera, III in 19 species and 6 genera, IV in 87 species and 6 genera.

The range in midbody scale rows is from 10 (three species of *Herpetodryas-Chironius*) to 45 (*Spalerosophis microlepis*). The maximum span is 11 (*Homalopsis buccata*).

TABLE 41. Distribution of character states of the number of midbody scale rows.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Classes[1] | 2–4 | 5–8 | 9–22 | 1 |
| | | SPECIES | | |
| Colubridae —1,000 | 77.9% | 11.5% | 1.9% | 8.7% |
| Elapidae — 138 | 79.0 | 8.0 | | 13.0 |
| Hydrophiidae— 50 | 20.0 | 14.0 | 66.0 | |
| Viperinae — 37 | 27.0 | 48.6 | 24.3 | |
| Crotalinae — 45 | 20.0 | 68.9 | 11.1 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 16[2] | 18.8 | 68.8 | 12.5 | |
| | | GENERA | | |
| Colubridae — 200 | 79.5 | 14.5 | 3.0 | 3.0 |
| Elapidae — 28 | 78.6 | 14.3 | | 7.1 |
| Hydrophiidae— 16 | 12.5 | 31.3 | 56.3 | |
| Viperinae — 8 | 12.5 | 50.0 | 37.5 | |
| Crotalinae — 6 | | 83.3 | 13.7 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | | 100.0 | | |

[1] See Table 40.

[2] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Elapidae—This family has States I, II, and IV in a sample of 138 species and 28 genera. State I occurs in 109 species and 22 genera, II in 11 species and 4 genera, IV in 18 species and 2 genera.

The range is from 13 (18 species of 6 genera) to 25 (*Naja naja, N. nigricollis*). The maximum span is 9 (*Naja naja, N. nigricollis*).

Hydrophiidae—The sea snakes have States I, II, and III in a sample of 50 species of the 16 genera. State I occurs in 10 species and 2 genera, II in 7 species and 5 genera, III in 33 species and 9 genera.

The range is from 15 (*Emydocephalus annulatus*) to 93 (*Kolpophis annandalei*). The maximum span is 27 (*Hydrophis ornatus*).

Viperinae—The true vipers have States I, II, and III in a sample of 37 species of the 8 genera. State I occurs in 10 species and 1 genus, II in 18 species and 4 genera, III in 9 species and 3 genera.

The range is from 15 (*Atheris hispidus, A. squamiger, Causus lichtensteini*) to 41 (*Bitis arietans, B. nasicornis*). The maximum span is 13 (*Bitis arietans*).

Crotalinae—The pit vipers have States I, II, and III in a sample of 45 species of the 6 genera. State I occurs in 9 species, II in 31 species and 5 genera, III in 5 species and 1 genus.

The range is from 17 (*Agkistrodon hypnale, A. nepa*) to 37 (*Lachesis mutus*). The maximum span is 9 (*Crotalus durissus, C. ruber, C. viridis, Trimeresurus monticola*).

*Azemiops* has State I.

*Atractaspis* has States I, II, and III in a sample of 16 species. The range is from 19 (4 species) to 37 (*microlepidota*). The maximum span is 15 (*microlepidota*).

## PHYLETICS OF CHARACTER 16

Character States II, III, and IV are rare in the colubrids (table 41) (Criterion 2).

State II occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Boaedon lineatus*
  - *Boiga blandingi*
    - *cynodon*
    - *dendrophila*
    - *irregularis*
  - *Bothrophthalmus lineatus*
  - *Chironius carinatus*
    - *fuscus*
  - *Coluber florulentus*
    - *hippocrepis*
  - *Cryophis hallbergi*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Elaphe carinatus*
    - *dione*
    - *guttata*
    - *mandarina*
    - *obsoleta*
    - *schrencki*
    - *taeniura*
    - *vulpina*
  - *Enhydris bocourti*
    - *chinensis*
    - *enhydris*
  - *Gonyosoma oxycephalum*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Holuropholis olivaecus*
  - *Hydraethiops melanogaster*
  - *Hypsiglena torquata*
  - *Lampropeltis getulus*
    - *triangulus*
  - *Lamprophis aurora*
  - *Leptodeira maculata*
    - *septentrionalis*
  - *Lioheterodon madagascariensis*
  - *Lycodonomorphus bicolor*
  - *Macropisthodon rudis*
  - *Natrix anoscopus*
    - *erythrogaster*
    - *rhombifera*
    - *sipedon*
  - *Pituophis deppei*
  - *Pseustes poecilonotus*
  - *Rhacidelus brazili*
  - *Scaphiophis albopunctatus*
  - *Trimorphodon lambda*
- Elapidae
  - *Acanthophis antarcticus*
  - *Dendroaspis polylepis*
  - *Naja naja*
    - *nigricollis*
  - *Oxyuranus scutellatus*
  - *Walterinnesia aegyptia*
- Hydrophiidae
  - *Acalyptophis peronii*
  - *Aipysurus laevis*
  - *Hydrelaps darwiniensis*

*Laticauda colubrina*
  *schistorhynchus*
  *semifasciata*
Viperinae
  *Adenorhinos barbouri*
  *Atheris hindii*
    *nitschei*
    *superciliaris*
  *Bitis cornutus*
    *heraldica*
    *peringueyi*
    *worthingtoni*
  *Cerastes vipera*
  *Eristicophis macmahoni*
  *Vipera ammodytes*
    *aspis*
    *berus*
    *lebetina*
    *persica*
    *xanthina*
Crotalinae
  *Agkistrodon bilineatus*
    *contortrix*
    *piscivorus*
  *Bothrops atrox*
    *barnetti*
    *cotiara*
    *dunni*
    *jararacussu*
    *lansbergii*
    *neuwiedi*
    *nummifer*
    *schlegeli*
  *Crotalus adamanteus*
    *atrox*
    *basiliscus*
    *cerastes*
    *horridus*
    *lepidus*
    *mitchellii*
    *molossus*
    *pusillus*
    *viridis*
  *Sistrurus catenatus*
    *miliarius*
  *Trimeresurus jerdoni*
    *monticola*
    *mucrosquamatus*
    *okinavensis*
    *puniceus*
    *wagleri*

*Atractaspis bibroni*
    *corpulenta*
    *irregularis*

In these colubrids this character state has a higher frequency of correlation with derived states of three other characters compared to the frequency distribution of these states of the same three characters in the total sample (table 42) (Criterion 3).

Also, these colubrids have a larger number of species confined to the terrestrial habitat (46.9 per cent) compared to the relative abundance of terrestrial colubrid species in the total working sample (36.2 per cent—table 43) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State III, highest numbers of midbody scale rows (table 40), occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
  *Arizona elegans*
  *Elaphe flavirufus*
    *subocularis*
  *Homalopsis buccata*
  *Natrix cyclopion*
    *taxispilota*
  *Pituophis melanoleucus*
    *sayi*
  *Pseudaspis cana*
  *Spalerosophis diadema*

- Hydrophiidae
  - *Astrotia stokesii*
  - *Enhydrina schistosa*
  - *Hydrophis* (16 species)
  - *Kolpophis annandalei*
  - *Lapemis curtus*
    - *hardwickii*
  - *Microcephalophis cantoris*
    - *gracilis*
  - *Pelamis platurus*
  - *Thalassophina viperina*
  - *Thalassophis anomalus*
- Viperinae
  - *Atheris chlorechis*
  - *Bitis arietans*
    - *atropos*
    - *gabonica*
    - *nasicornis*
  - *Cerastes cerastes*
  - *Echis carinata*
    - *coloratus*
  - *Vipera russelii*
- Crotalinae
  - *Bothrops alternatus*
  - *Crotalus durissus*
    - *ruber*
  - *Lachesis muta*
  - *Trimeresurus flavoviridis*
- *Atractaspis dahomeyensis*
  - *microlepidota*

In these colubrids this character state has a higher frequency of correlation with derived states of 10 other characters compared to the frequency distribution of these states of the same 10 characters in the total sample (table 42) (Criterion 3).

Also, these colubrids have a markedly larger number of species confined to the terrestrial and aquatic habitats (60.0 per cent, 30.0 per cent) compared to the relative abundance of terrestrial and aqua-

TABLE 42. Correlation of States II, III, and IV of Character 16 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State II of Character 16 | In species having State III of Character 16 | In species having State IV of Character 16 | In total working sample |
| 1 | | 40.0% (3) | 66.7% (2) | 14.3% (28) |
| 2 | | 40.0 (3) | | 15.6 (31) |
| 7 | | | 100.0 (4) | 25.5 (56) |
| 9 | | 30.0 (3) | 55.6 (1) | 6.8 (14) |
| 11 | | 40.0 (3) | 66.7 (2) | 26.7 (50) |
| 12 | | 40.0 (4) | | 4.8 (13) |
| 13 | | | 66.7 (3) | 31.8 (54) |
| 14 | | | 33.3 (2) | 3.5 (7) |
| 17 | 53.1% (12)* | 80.0 (5) | | 35.4 (48) |
| 19 | | | 66.7 (2) | 36.8 (68) |
| 20 | 63.3 (17) | 60.0 (4) | | 41.2 (74) |
| 22 | | | 44.4 (2) | 4.5 (11) |
| 28 | | | 66.7 (1) | 11.7 (26) |
| 37 | | 40.0 (3) | | 22.9 (54) |
| 38 | | | 75.0 (2) | 16.2 (27) |
| 39 | | 30.0 (3) | | 9.0 (15) |
| 40 | | | 44.4 (3) | 24.8 (54) |
| 47 | 61.7 (16) | 80.0 (5) | 100.0 (4) | 48.5 (84) |
| 50 | | | 57.1 (1) | 20.0 (24) |

* Number of genera.

TABLE 43. Habitat distribution of colubrid species having States II, III, and IV of Character 16 compared to the total colubrid working sample.

| | Total Working Sample | STATES | | |
|---|---|---|---|---|
| | | II | III | IV |
| Terrestrial | 36.2% | 46.9% | 60.0% | |
| Arboreal | 16.5 | 22.4 | | 11.1% |
| Aquatic | 14.9 | 18.4 | 30.0 | |
| Subterrestrial | 10.8 | 4.1 | | 11.1 |
| Fossorial | 12.4 | 2.0 | 10.0 | 75.8 |
| Variation | 5.3 | 4.1 | | |
| Unknown | 3.5 | 2.0 | | |

tic colubrid species in the total sample (36.2 per cent, 14.9 per cent—table 43) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

The serial nature of scale rows makes a single trend in the arrangement of these two states most probable (fig. 16). This is further supported by the correlation of States II and III with derived states of the same characters (table 42) and with concordant predominance in the same habitat zones (table 43).

State IV, a low number of midbody scale rows (table 40), occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Calamaria leucogaster*
  - *linnaei*
  - *pavimentata*
  - *schlegeli*
  - *septentrionalis*
- *Carphophis amoena*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Dryccalamus davisoni*

Elapidae
- *Dendroaspis viridis*
- *Elapsoidea sundevalli*
- *Maticora bivirgata*
- *Pseudohaje nigra*
- *Ultrocalamus preussi*

In these colubrids this character state has a higher frequency of correlation with derived states of 13 other characters compared to the frequency distribution of these states of the same 13 characters in the total sample (table 42) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to fossorial habitats (75.8 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent—table 43) (Criterion 5).

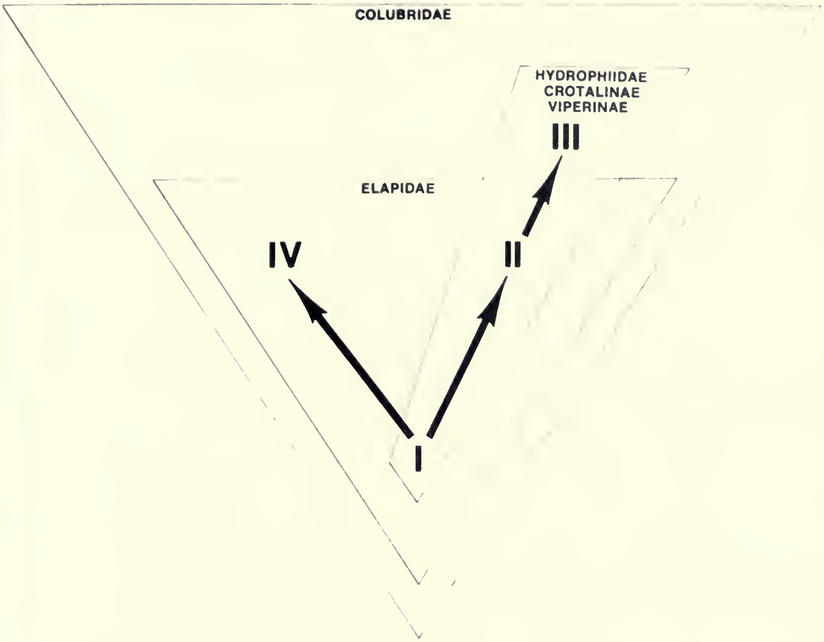

FIG. 16. Distribution among families of states of Character 16. Direction of change among states shown by arrows.

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State IV probably arose in a different direction from States II and III because State IV correlates with many derived states of different characters (table 42) and is predominantly more abundant in snakes of different habitat zones (table 43).

Our interpretation of the phyletics of Character 16 is shown in Figure 16.

## Character 17—Dorsal Scales Smooth or Keeled

### Description of Character

The dorsal scales are those scales situated on the sides and dorsum along the body and tail.

Three states are recognized:

State I —dorsals smooth
State II —intraspecific variation, both States I and III present

TABLE 44. Distribution of character states of the scalation of dorsal scales.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | |
| Description | Smooth | Intraspecific Variation | Keeled | |
| | | SPECIES | | |
| Colubridae[1] —886 | 69.2% | 6.5 | 24.3 | |
| Elapidae[1] —134 | 96.3 | 1.5 | 2.2 | |
| Hydrophiidae[2] — 42 | 45.2 | 26.2 | 28.6 | |
| Viperinae[3] — 38 | | | 100.0 | |
| Crotalinae[3] — 45 | 2.2 | | 97.8 | |
| *Azemiops*[3] — 1 | 100.0 | | | |
| *Atractaspis*[4] — 16 | 100.0 | | | |
| | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —193 | 69.4 | 11.9 | 18.7 | |
| Elapidae — 28 | 82.1 | 7.1 | 10.7 | |
| Hydrophiidae — 16 | 50.0 | | 37.5 | 12.5 |
| Viperinae — 8 | | | 100.0 | |
| Crotalinae — 6 | | | 83.3 | 16.7 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

State III—each dorsal scale with a longitudinal central keel

Some species may have only the outer lateral row or rows smooth; they are referred to State III. Some species may have the posterior dorsal scales keeled and the anterior smooth; they are scored as State II. Some species have specimens with keeled dorsal scales and other specimens with smooth dorsal scales; these species are also rated as State II.

### Familial Ranges of Variation (Table 44)

Colubridae—This family has all three states in a sample of 886 species of 193 genera. State I occurs in 613 species of 134 genera, II in 58 species of 23 genera, III in 215 species of 36 genera.

Elapidae—This family has all three states in a sample of 134 species of 28 genera. State I occurs in 129 species of 23 genera, II in 2 species of 2 genera, III in 3 species of 3 genera.

Hydrophiidae—The sea snakes have all three states in a sample of 42 species of the 16 genera. State I occurs in 19 species of 8 genera, II in 11 species of 2 genera, III in 12 species of 6 genera.

Viperinae—The true vipers only have State III in a sample of 38 species of the 8 genera.

Crotalinae—The pit vipers have States I and III in a sample of 45 species of the 6 genera. State I occurs in a single *Agkistrodon*, III in 44 species of 6 genera.

*Azemiops* and *Atractaspis* have State I.

## PHYLETICS OF CHARACTER 17

Character State III, keeled dorsals, is not particularly rare in the colubrids (table 44). It occurs in the following 92 colubrids (plus other taxa):

- Colubridae
  - *Achalinus spinalis*
  - *Bothrophthalmus lineatus*
  - *Cryophis hallbergi*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Dispholidus typus*
  - *Drymobius bifossatus*
    - *margaritiferus*
  - *Elaphe carinata*
    - *dione*
    - *flavirufa*
    - *frenatus*
    - *guttata*
    - *obsoleta*
    - *schrencki*
    - *subocularis*
    - *taeniura*
    - *vulpina*
  - *Gastropyxis smaragdina*
  - *Haldea striatula*
  - *Hapsidophrys lineata*
  - *Helicops angulatus*
    - *carinicauda*
    - *leopardinus*
    - *schistosus*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Holarchus formosanus*
    - *hainonensis*
  - *Homalopsis buccata*
  - *Hydraethiops melanogaster*
  - *Leptophis mexicanus*
    - *occidentalis*
  - *Macrophisthodon rudis*
  - *Mehelya capensis*
    - *chanleri*
    - *poensis*
  - *Natrix*—all 20 species examined
  - *Ninia atrata*
    - *sebae*
  - *Opheodrys aestivus*
  - *Opisthotropis kuatunensis*
    - *latouchi*
  - *Oxybelis fulgidus*
  - *Phyllorhynchus decurtatus*
  - *Pituophis deppei*
    - *melanoleucus*
    - *sayi*
  - *Pseudoxenodon sinensis*
    - *striaticaudatus*
  - *Pseustes poecilonotus*
    - *sulphureus*
  - *Spilotes pullnlatus*
  - *Storeria dekayi*
    - *occipitomaculata*
  - *Thamnophis*—all 7 species examined
  - *Thelotornis kirtlandii*
  - *Thrasops flavigularis*
  - *Tretanorhinus mocquardii*
    - *variabilis*
  - *Tropidocloniom lineatum*
  - *Tropidodipsas fischeri*
    - *philippi*
  - *Zaocys dhumnades*
    - *nigromarginatus*
- Elapidae
  - *Acanthophis antarcticus*

*Hemachatus haemachatus*
Hydrophiidae
*Acalyptophis peronii*
*Astrotia stokesii*
*Enhydrina schistosa*
*Ephalophis greyi*
*Hydrophis caerulescens*
*fasciatus*
*inornatus*
*kingi*
*majori*
*mamillaris*
*Kerilia jerdoni*
*Thalassophis anomalus*
Viperinae—all taxa
Crotalinae
*Agkistrodon*, 8 species
(but *A. rhodostoma*)
*Bothrops* (all)
*Crotalus* (all)
*Lachesis*
*Sistrurus* (all)
*Trimeresurus* (all)

These colubrids have a significantly larger number of species confined to the aquatic habitat (33.7 per cent) compared to the relative abundance of aquatic colubrid species in the remainder of the working sample (14.9 per cent) (table 45) (Criterion 5). Conversely there are relatively fewer fossorial species with keeled scales than in the total working sample (table 45). The ecological relationships are strongly supported in the distribution of scale types among the elapids and hydrophiids. Keeling is rare in the basically secretive elapids, yet occurs in about half of their presumptive aquatic offshoots, the hydrophiids. The ecological distributional correlation makes functional sense, since keels would add unnecessary friction to the movements of secretive snakes and provide helpful additional surface area to swimming snakes.

Also, there is a markedly larger number of colubrid species from the United States (30.4 per cent) and western Asia (22.8 per cent) compared to the relative abundance of colubrids from these same areas (17.1 per cent; 10.8 per cent) in the total working sample (Criterion 6).

The application of two criteria (5, 6) suggests that this state is derived (Criterion 8).

TABLE 45. Habitat distribution of colubrid species having State III of Character 17 compared to the total colubrid sample.

| | Total Working Sample | State III Character 17 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 37.0 |
| Arboreal | 16.5 | 13.0 |
| Aquatic | 14.9 | 33.7 |
| Subterrestrial | 10.8 | 10.9 |
| Fossorial | 12.4 | 1.1 |
| Variation | 5.3 | 4.3 |
| Unknown | 3.5 | |

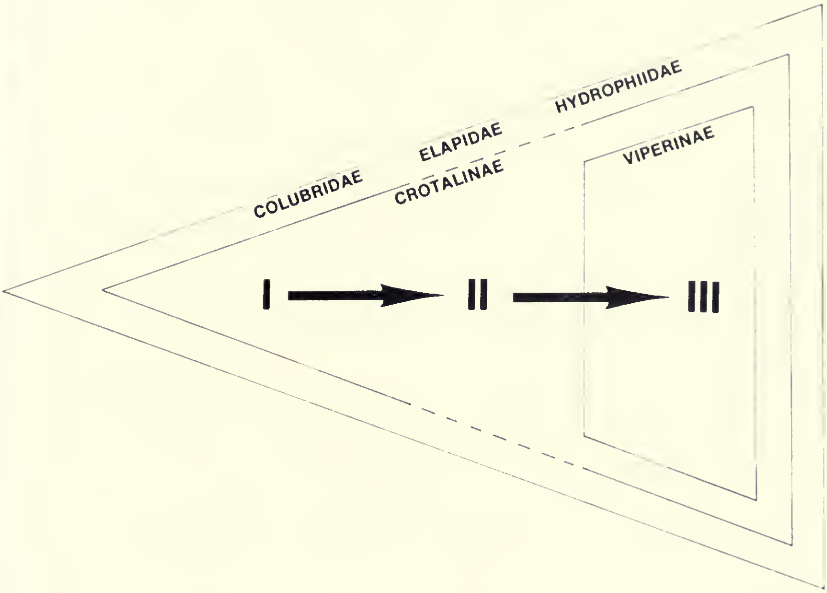

FIG. 17. Distribution among families of states of Character 17. Direction of change among states shown by arrows.

State II is an intermediate sequential state by definition. The taxa with State II are:

- Colubridae
  - *Amastridium veliferum*
  - *Aspidura trachyprocta*
  - *Chironius carinatus*
    - *fuscus*
  - *Chrysopelea ornata*
  - *Crotaphopeltis hotamboeia*
  - *Gonyosoma oxycephalum*
  - *Haldea valeriae*
  - *Liodytes alleni*
  - *Lytorhynchus maynardi*
  - *Opheodrys major*
  - *Oxybelis aeneus*
    - *brevirostris*
  - *Ptyas korros*
    - *mucosus*
  - *Pythonodipsas carinatus*
  - *Rhinobothryum bovallii*
  - *Spalerosophis diadema*
- Elapidae
  - *Aspidelaps scutatus*
  - *Walterinnesia aegyptia*
- Hydrophiidae
  - *Aipysurus duboisii*
    - *laevis*
  - *Hydrophis belcheri*
    - *brookii*
    - *cyanocinctus*
    - *klossi*
    - *lapemoides*
    - *melanocephalus*
    - *melanosoma*
    - *ornatus*
    - *torquatus*

Our interpretation of the phyletics of Character 17 is shown in Figure 17.

## Character 18—Serrated Keels on Lateral Scales

### DESCRIPTION OF CHARACTER

When the lateral scales are keeled they may be serrated (Gans, 1959, figs. 3–5). The absence of serrated keels where the lateral scales are smooth (Character 17, State I) is a necessary correlate in taxa lacking keeled scales. Therefore, we only considered taxa that have the lateral scales keeled.

Two states are recognized:

State I —serration absent
State II —serration present

### FAMILIAL RANGES OF VARIATION (Table 46)

Colubridae—This family has both states plus the necessary correlate in a sample of 886 species of 193 genera. State I occurs in 272 species of 58 genera, II in a single species of *Dasypeltis* (Boulenger, 1894). Gans (1959) recognized five species of *Dasypeltis,* all having serrated keels. The necessary correlate occurs in 613 species of 134 genera.

Elapidae—This family has State I and the necessary correlate in a sample of 134 species and 28 genera. State I occurs in 5 species and 5 genera. The necessary correlate occurs in 129 species of 23 genera.

Hydrophiidae—The sea snakes has State I and the necessary correlate in a sample of 42 species and 16 genera. State I occurs in 19 species and 8 genera. The necessary correlate occurs in 23 species and 8 genera.

Crotalinae—The pit vipers has State I and the necessary correlate in a sample of 45 species of the 6 genera. State I occurs in 44 species of the 6 genera. The necessary correlate occurs in a single *Agkistrodon.*

Viperinae—The true vipers have States I and II in a sample of 38 species of the 8 genera. State I occurs in 32 species of 6 genera, II in 6 species of 3 genera. Intrageneric variation occurs in *Atheris.*

*Azemiops* and *Atractaspis* have the necessary correlate.

### PHYLETICS OF CHARACTER 18

State II is extremely rare in the colubrids (table 46), occurring only in the genus *Dasypeltis* (Criterion 2).

TABLE 46. Distribution of character states in keeled serration of lateral scales.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | | nc[5] |
| Description | Lateral scales without serrated keels | Lateral scales with serrated keels | | Scales smooth |
| | SPECIES | | | |
| Colubridae[1] —886 | 30.7% | 0.1% | | 69.2% |
| Elapidae[1] —134 | 3.7 | | | 96.3 |
| Hydrophiidae[2]— 42 | 45.2 | | | 54.8 |
| Viperinae[3] — 38 | 84.2 | 15.8 | | |
| Crotalinae[3] — 45 | 97.8 | | | 2.2 |
| *Azemiops*[3] — 1 | | | | 100.0 |
| *Atractaspis*[4] — 16 | | | | 100.0 |
| | GENERA | | INTRAGENERIC VARIATION | |
| Colubridae —193 | 32.8 | 0.5 | | 66.7 |
| Elapidae — 28 | 17.9 | | | 82.1 |
| Hydrophiidae — 16 | 50.0 | | | 50.0 |
| Viperinae — 8 | 62.5 | 25.0 | 12.5% | |
| Crotalinae — 6 | 100.0 | | | |
| *Azemiops* — 1 | | | | 100.0 |
| *Atractaspis* — 1 | | | | 100.0 |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; deWitte, 1959; Perret, 1960.

[5] Necessary correlate of Character 17, State I.

State II, serrated lateral scales, occurs in the following colubrids (plus other taxa) in our sample:

Colubridae
- *Dasypeltis fasciatus*
  - *inornata*
  - *scabra*

Viperinae
- *Atheris ceratophorus*
  - *nitschei*
- *Cerastes cerastes*
  - *vipera*
- *Echis carinatus*
  - *coloratus*

This state is thus found in arboreal, tropical African snakes (*Atheris, Dasypeltis*) and in arid or semi-arid inhabitants of North Africa and Southwest Asia.

We feel that it is legitimate to characterize serrated lateral keels as a morphological specialization (Criterion 4). This specialization may be regarded as one of several analogues for the production of a rasping or hissing noise, whose effect is to warn or startle potential enemies. In *Echis* and *Cerastes* loops of the body are drawn past one another and the special scales apparently rub together to produce the noise. A fantastic parallel is found in the scales and behavior of the defenseless egg-eating snake *Dasypeltis*, which also mimics the African viperines in coloration (Gans and Richmond, 1957).

Similar noises are made in the puffing and hissing behavior of some of the heavy-bodied vipers, and by the rattles in *Crotalus* (Klauber, 1956). A correlation with arenicolous habits is suggested by the distribution of such features; the impression of habitat influence is reinforced by the occurrence of a rasp-making device in *Teratoscincus*, a gecko of arid, central Asia (Mebs, 1966).

The application of two criteria (2, 4) suggests that this state is derived (Criterion 8).

Our interpretation of the phyletics of Character 18 is shown in Figure 4.

## Character 19—Apical Pits

At the posterior extremity of each dorsal scale there may be a small single or pair of apical pits (Underwood, 1967, p. 41). Other probably sensory pits and tubercles appear on head shields as well as the dorsal scales. Our analysis is restricted to the dorsal scales so that data from G. A. Boulenger (1893, 1894, 1896) can be used.

TABLE 47. Distribution of character states of the apical pits.

| | | STATES | | | |
|---|---|---|---|---|---|
| | | I | II | III | |
| Description | | Absent | Intraspecific Variation | Present | |
| | | | SPECIES | | |
| Colubridae[2] | —972 | 39.0% | 10.9% | 50.1% | |
| Elapidae[2] | —133 | 100.0 | | | |
| Hydrophiidae[3] | — 42 | 100.0 | | | |
| Viperinae[4] | — 38 | | | 100.0 | |
| Crotalinae[4] | — 45 | 4.4 | | 95.6 | |
| *Azemiops* [1,4] | — 1 | | 100.0 | | |
| *Atractaspis*[5] | — 16 | 100.0 | | | |
| | | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | —192 | 49.0 | 2.6 | 48.4 | |
| Elapidae | — 27 | 100.0 | | | |
| Hydrophiidae | — 16 | 100.0 | | | |
| Viperinae | — 8 | | | 100.0 | |
| Crotalinae | — 6 | | | 83.3 | 16.7 |
| *Azemiops* | — 1 | | 100.0 | | |
| *Atractaspis* | — 1 | 100.0 | | | |

[1] Present on dorsal neck region.

[2] Boulenger, 1893–96.

[3] M. A. Smith, 1926, 1931.

[4] Working sample.

[5] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Three states are recognized:

State I —pits absent

State II —intraspecific variation, both States I and III present

State III—pits present

### Familial Ranges of Variation (Table 47)

Colubridae—This family has all three states in a sample of 972 species of 192 genera. State I occurs in 379 species of 94 genera, II in 106 species of 5 genera, III in 487 species of 93 genera.

Elapidae, Hydrophiidae—All taxa in these two families have State I in a sample of 175 species (133, 42) of 43 genera (27, 16).

Viperinae—The true vipers all have State III in a sample of 38 species of the 8 genera.

Crotalinae—The pit vipers have States I and III in a sample of 45 species of the 6 genera. State III occurs in 43 species of the 6 gen-

TABLE 48. Correlation of States I and III of Character 19 with derived states of the other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | | | |
|---|---|---|---|---|---|---|
| | In species having State I of Character 19 | | In species having State III of Character 19 | | In total working sample | |
| 1 | 26.9% | (18)* | 7.9% | (9) | 14.3% | (28) |
| 2 | 11.1 | (9) | 19.0 | (21) | 15.6 | (31) |
| 3 | 1.9 | (2) | 0.5 | (1) | 0.1 | (3) |
| 4 | 0.9 | (1) | 5.3 | (2) | 3.8 | (4) |
| 5 | 5.6 | (5) | 2.7 | (4) | 3.5 | (9) |
| 6 | 0 | | 0 | | 0 | |
| 7 | 39.8 | (32) | 17.5 | (20) | 25.5 | (56) |
| 8 | 0 | | 0 | | 0 | |
| 9 | 11.2 | (7) | 4.8 | (7) | 6.8 | (14) |
| 10 | 0 | | 0 | | 0.6 | (1) |
| 11 | 22.4 | (16) | 31.0 | (27) | 26.7 | (50) |
| 12 | 4.6 | (5) | 5.3 | (8) | 4.8 | (13) |
| 13 | 28.0 | (8) | 34.8 | (28) | 31.8 | (54) |
| 14 | 1.9 | (2) | 4.3 | (4) | 3.5 | (7) |
| 15 | 0 | | 0 | | 0 | |
| 16 | 13.9 | (9) | 26.5 | (24) | 21.7 | (34) |
| 17 | 34.3 | (20) | 34.6 | (20) | 35.4 | (48) |
| 18 | 0 | | 5.3 | (4) | 0.1 | (3) |
| 20 | 29.6 | (24) | 47.3 | (55) | 41.2 | (74) |
| 21 | 6.7 | (5) | 24.9 | (30) | 18.9 | (29) |
| 22 | 8.3 | (7) | 2.1 | (3) | 4.5 | (11) |
| 23 | 0 | | 2.6 | (4) | 1.9 | (5) |
| 24 | 3.7 | (3) | 4.2 | (8) | 3.8 | (11) |
| 25 | 7.5 | (4) | 6.3 | (8) | 6.3 | (12) |
| 26 | 9.1 | (6) | 11.9 | (12) | 12.6 | (19) |
| 27 | 12.4 | (9) | 19.7 | (28) | 17.9 | (40) |
| 28 | 22.3 | (16) | 6.5 | (11) | 11.7 | (26) |
| 29 | 14.9 | (14) | 7.2 | (11) | 10.1 | (27) |
| 30 | 12.6 | (10) | 3.4 | (4) | 6.3 | (15) |
| 31 | 18.2 | (15) | 18.5 | (25) | 19.5 | (44) |
| 32 | 40.7 | (27) | 20.7 | (10) | 26.3 | (55) |
| 33 | 53.8 | (34) | 34.8 | (19) | 43.0 | (76) |
| 34 | 16.5 | (14) | 1.6 | (3) | 6.8 | (18) |
| 35 | 3.8 | (4) | 1.1 | (2) | 2.0 | (6) |
| 36 | 14.3 | (13) | 2.1 | (3) | 6.1 | (16) |
| 37 | 29.6 | (26) | 19.6 | (25) | 22.9 | (54) |
| 38 | 31.3 | (18) | 9.3 | (7) | 16.2 | (27) |
| 39 | 19.7 | (10) | 4.2 | (4) | 9.0 | (15) |
| 40 | 23.6 | (20) | 25.9 | (30) | 24.8 | (54) |
| 41 | 16.9 | (10) | 8.1 | (9) | 10.9 | (20) |
| 42 | 20.6 | (12) | 3.3 | (2) | 8.7 | (14) |
| 43 | 3.8 | (2) | 1.1 | (2) | 1.9 | (3) |
| 44 | 8.6 | (6) | 4.9 | (5) | 5.8 | (11) |
| 45 | 11.4 | (5) | 26.3 | (14) | 19.5 | (21) |
| 46 | 21.7 | (17) | 32.3 | (34) | 26.9 | (52) |
| 47 | 53.8 | (37) | 64.7 | (71) | 48.5 | (84) |
| 48 | 7.1 | (5) | 5.6 | (6) | 6.2 | (11) |
| 49 | 27.1 | (14) | 10.1 | (11) | 15.5 | (26) |
| 50 | 39.4 | (15) | 9.9 | (7) | 20.0 | (24) |

* Number of genera.

era, I occurs in 2 species of *Trimeresurus*. Intrageneric variation occurs in *Trimeresurus*.

*Atractaspis* has State I; *Azemiops*, State II.

### Phyletics of Character 19

Unlike all the other characters in our analysis, this one shows no marked differences in proportions of species of colubrids in the two principal states (table 47). We have nevertheless included the character, relying on its correlations with other characters and a reverse use of morphological specialization in relation to ecology to decide phyletic direction.

For 36 of the 43 characters having derived states occurring in the Colubridae there were sufficient numbers in our samples to compare the distributions of species having State I and State III (table 48). In 16 of 36 characters chi-square tests indicated no significant difference in the proportions of species in State I and State III. In three characters, there was a significantly higher ($P < .01$–$.001$) proportion of species having State III than in the rest of the sample. In 17 characters, species having State I were significantly more abundant compared to the rest of the sample. Applying these data as Criterion 3, State I, absence of apical pits, is derived.

The absence of apical pits on the dorsal scales occurs in the following 108 colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Abastor erythrogrammus*
  - *Achalinus spinalis*
  - *Amastridium veliferum*
  - *Aparallactus lunulatus*
    - *werneri*
  - *Apostolepis ambinigra*
  - *Arrhyton taeniatum*
    - *vittatum*
  - *Aspidura trachyprocta*
  - *Atractus elaps*
    - *erythromelas*
    - *latifrons*
    - *ventrimaculatus*
  - *Bothrophthalmus lineatus*
  - *Brachyorrhus albus*
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Carphophis amoena*
  - *Chilorhinophis carpenteri*
  - *Coniophanes fissidens*
  - *Conophis lineatus*
  - *Cryophis hallbergi*
  - *Darlingtonia haetiana*
  - *Dimades plicatilis*
  - *Drepanoides eatonii*
  - *Dromicodryas bernieri*
  - *Dugandia bicolor*
  - *Elapomorphus blumii*
  - *Enhydris bocourti*
    - *chinensis*
    - *enhydris*
    - *plumbea*
  - *Erythrolamprus aesculapii*
  - *Farancia abacura*

- *Geophis multitorques*
  - *semidoliatus*
- *Grayia smithi*
- *Haldea striatula*
  - *valeriae*
- *Helicops angulatus*
  - *carinicauda*
  - *leopardinus*
  - *schistosus*
- *Homalopsis buccata*
- *Hydraethiops melanogaster*
- *Hydrodynastes gigas*
- *Hydrops triangularis*
- *Lamprophis aurora*
- *Limnophis bicolor*
- *Liopeltis tricolor*
- *Liophis anomala*
  - *cobella*
  - *miliaris*
- *Lycodonomorphus bicolor*
- *Lygophis boursieri*
  - *flavifrenatus*
  - *lineatus*
- *Lytorhynchus diadema*
  - *maynardi*
- *Macrocalamus lateralis*
- *Manolepis putmani*
- *Mehelya capensis*
  - *chanleri*
  - *poensis*
- *Miodon gabonensis*
- *Natriciteres olivacea*
- *Opheodrys major*
- *Opisthotropis kuatunensis*
  - *latouchi*
- *Passerita mycterizans*
  - *nasuta*
  - *prasinus*
- *Phyllorhynchus decurtatus*
- *Psammodynastes pictus*
  - *pulverulentus*
- *Pseudorabdion collaris*
  - *longiceps*
- *Pseudoxenodon sinensis*
  - *striaticaudatus*
- *Rhadinaea brevirostris*
  - *decorata*
  - *seperaster*
- *Scaphiodontophis annulatus*
- *Sibon sibon*
- *Sibynomorphus turgidus*
- *Stegonotus borneensis*
  - *magnus*
- *Stenorhina degenhardti*
- *Stilostoma extenuatum*
- *Storeria dekayi*
  - *occipitomaculata*
- *Tantilla gracilis*
- *Thamnophis butleri*
  - *eques*
  - *marcianus*
  - *macrostemma*
  - *radix*
  - *sauritus*
  - *sirtalis*
- *Tretanorhinus mocquardi*
  - *variabilis*
- *Tropidocloniom lineatum*
- *Tropidodipsas fischeri*
  - *philippi*

Elapidae—all taxa
Hydrophiidae—all taxa
Crotalinae

- *Trimeresurus sumatranus*
  - *wagleri*

The apical pitless colubrids have a markedly larger number of species of aquatic and secretive habits (68.5 per cent) compared to the aquatic, subterrestrial, and fossorial colubrid species in the total sample (38.1 per cent) (table 49) (Criterion 5). When State I or III species are compared as independent samples to the remainder, the chi-square test of the proportional distribution among habitat types is highly significant ($P < .001$). By themselves, these results give no basis for a decision. However, disappearance of the pits in various taxa as a consequence of adopting underground or aquatic

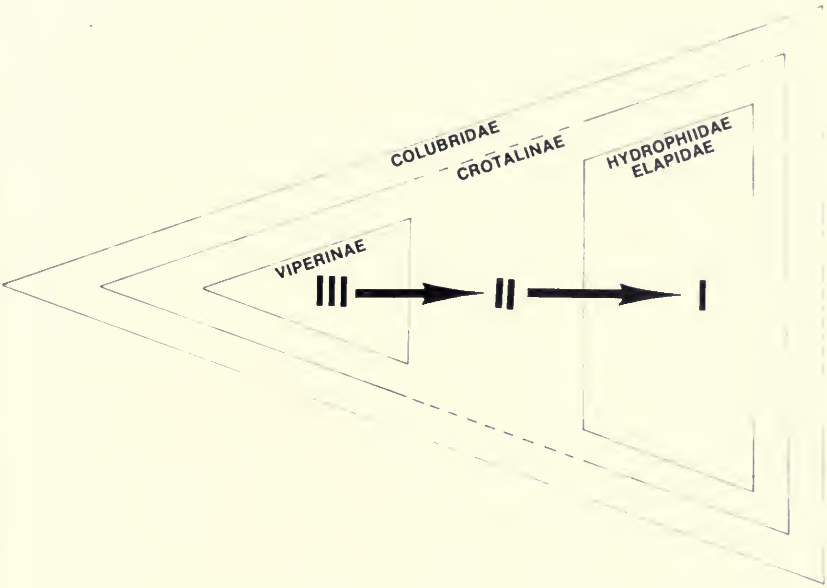

FIG. 18. Distribution among families of states of Character 19. Direction of change among states shown by arrows.

habits appears more likely and logical than the identical development of a specialized structure in a multitude of different taxa. Such an ecotypic correlation is supported by the total absence of pits in the basically cryptic elapids and their presumptive aquatic offshoots, the hydrophiids. From this argument and the preceding, we regard State I, absence of apical pits, as derived.

State II is an intermediate sequential state because each taxon with this state has both States, I and III. The taxa having State II in our working sample are the colubrids *Gastropyxis smaragdina* and *Liodytes alleni.*

TABLE 49. Habitat distribution of colubrid species having States I and III of Character 19 compared to the total colubrid working sample.

| | Total Working Sample % | State I Character 19 % | State III Character 19 % |
|---|---|---|---|
| Terrestrial | 36.2 | 19.4 | 45.0 |
| Arboreal | 16.5 | 5.6 | 22.8 |
| Aquatic | 14.9 | 25.0 | 9.5 |
| Subterrestrial | 10.8 | 18.5 | 6.3 |
| Fossorial | 12.4 | 25.0 | 5.3 |
| Variation | 5.7 | 2.8 | 7.0 |
| Unknown | 3.5 | 3.7 | 3.2 |

TABLE 50. Spans in number of ventrals by species and families.

| Span | Number of Species | | | | | |
|---|---|---|---|---|---|---|
| | All families | Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3,4] | Crotalinae[3] |
| 1 | 219 | 189 | 27 | 2 | | 1 |
| 2 | 11 | 10 | 1 | | | |
| 3 | 22 | 17 | 2 | 1 | 2 | |
| 4 | 11 | 8 | 2 | | | 1 |
| 5 | 21 | 16 | 3 | 1 | | 1 |
| 6 | 25 | 18 | 3 | 1 | 2 | 1 |
| 7 | 22 | 15 | 4 | 1 | | 2 |
| 8 | 25 | 21 | 3 | | 1 | |
| 9 | 32 | 26 | 4 | | 1 | 1 |
| 10 | 24 | 18 | 2 | 2 | 2 | |
| 11 | 25 | 19 | 2 | 2 | | 2 |
| 12 | 44 | 33 | 5 | | 4 | 2 |
| 13 | 29 | 27 | 1 | | | 1 |
| 14 | 40 | 33 | 5 | 1 | | 1 |
| 15 | 40 | 31 | 4 | 2 | 1 | 2 |
| 16 | 34 | 29 | 4 | | 1 | |
| 17 | 30 | 23 | 3 | 2 | 1 | 1 |
| 18 | 42 | 33 | 8 | | | 1 |
| 19 | 41 | 33 | 2 | 2 | 4 | |
| 20 | 34 | 30 | 1 | | 1 | 2 |
| 21 | 29 | 23 | 2 | | 3 | 1 |
| 22 | 29 | 22 | 5 | | 1 | 1 |
| 23 | 23 | 18 | | | 3 | 2 |
| 24 | 32 | 28 | 1 | | 1 | 2 |
| 25 | 21 | 19 | 1 | | 1 | |
| 26 | 22 | 16 | 1 | | | 5 |
| 27 | 23 | 18 | 3 | | | 2 |
| 28 | 17 | 15 | 2 | | | |
| 29 | 17 | 16 | | | | 1 |
| 30 | 16 | 14 | | | 1 | 1 |
| 31 | 25 | 18 | 3 | 1 | 1 | 2 |
| 32 | 14 | 11 | | | 1 | 2 |
| 33 | 14 | 10 | 1 | 1 | | 2 |
| 34 | 15 | 9 | 3 | | 2 | 1 |
| 35 | 10 | 5 | 3 | 1 | | 1 |
| 36 | 8 | 5 | | | 2 | 1 |
| 37 | 11 | 9 | 1 | 1 | | |
| 38 | 11 | 9 | 1 | | | 1 |
| 39 | 12 | 11 | | 1 | | |
| 40 | 12 | 9 | 3 | | | |
| 41 | 3 | 2 | 1 | | | |
| 42 | 11 | 8 | 1 | 2 | | |
| 43 | 11 | 5 | 4 | 2 | | |
| 44 | 5 | 3 | 2 | | | |
| 45 | 4 | 3 | | 1 | | |
| 46–50 | 20 | 15 | 3 | 1 | | 1 |
| 51–55 | 14 | 10 | 3 | 1 | | |
| 56–60 | 8 | 4 | 3 | 1 | | |

TABLE 50. Spans in number of ventrals by species and families (*continued*)

| | | Number of Species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3,4] | Crotalinae[3] |
| 61–65 | 6 | 2 | | 3 | 1 | |
| 66–70 | 9 | 4 | 2 | 3 | | |
| 76–80 | 5 | 1 | 2 | 2 | | |
| 81–85 | 3 | 1 | | 2 | | |
| 86–90 | 4 | 1 | | 3 | | |
| 93–94 | 2 | 1 | | 1 | | |
| 96 | 1 | 1 | | | | |
| 101–103 | 4 | 1 | | 3 | | |
| 116 | 1 | | | 1 | | |
| 128 | 1 | | | 1 | | |
| 191 | 1 | | | 1 | | |
| Totals | 1,245 | 976 | 137 | 50 | 37 | 45 |
| Span 40 or less | 90.9% | 93.6% | 84.7% | 44.0% | 97.3% | 97.8% |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Excluding *Azemiops* and *Atractaspis*.

Our interpretation of the phyletics of Character 19 is shown in Figure 18.

## Character 20—Number of Ventrals

### DESCRIPTION OF CHARACTER

Ventrals are the enlarged belly plates. Their counts are along the venter from the first enlarged plate near the head posteriorly to the anal plates. See Peters (1946, p. 378) for a description of ventrals and their count. The definition used here corresponds closely but not exactly with the post-Boulenger technique of Dowling (1951).

### CLASSES AND STATES

The total range of variation in number of ventrals is segmented by steps of 40, since a span of 40 covers most of the intraspecific variation encountered (90.9 per cent—table 50).

Four characters used in this study only have ranges given for each taxon (literature cited in table 50). Therefore, the mean of each taxon could not be determined from the literature. Our method of assigning taxa to a range is explained under Character 11. Seventeen classes resulted as shown in Table 51. Four states are recognized:

TABLE 51. Frequency distribution of species in range classes of number of ventrals in families of advanced snakes.

| | | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| Class | Range | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 97–136 | 82/15 | 9/3 | | 11/1 | 3/0 |
| 2 | Intermediate[2] | 39/15 | 1/3 | 2/1 | 5/3 | 4/1 |
| 3 | 137–176 | 409/70 | 38/7 | 9/3 | 20/3 | 21/1 |
| 4 | Intermediate | 58/21 | 3/2 | 3/2 | | 6/3 |
| 5 | 177–216 | 227/45 | 41/5 | 3/0 | 1/1 | 9/0 |
| 6 | Intermediate | 45/11 | 10/5 | 0/1 | | 2/1 |
| 7 | 217–256 | 95/19 | 26/3 | 7/3 | | |
| 8 | Intermediate | 6/1 | 2/1 | 1/1 | | |
| 9 | 257–296 | 14/1 | 4/0 | 3/1 | | |
| 10 | Intermediate | 1/0 | 1/0 | 4/0 | | |
| 11 | 297–336 | | 2/0 | 4/0 | | |
| 12 | Intermediate | | | 7/3 | | |
| 13 | 337–376 | | | 1/1 | | |
| 14 | Intermediate | | | 1/0 | | |
| 15 | 377–416 | | | 2/0 | | |
| 16 | Intermediate | | | 2/0 | | |
| 17 | 417–456 | | | 1/0 | | |
| Totals | | 976/198 | 137/29 | 50/16 | 37/8 | 45/6 |

[1] Excludes *Azemiops* and *Atractaspis*.

[2] See Character 11 text for explanation.

TABLE 52. Distribution of character states of the number of ventrals.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Classes[1] | 1 | 2–6 | 7–10 | 11–17 |
| | | SPECIES | | |
| Colubridae —976 | 8.4% | 79.7% | 11.9% | |
| Elapidae —137 | 6.6 | 67.9 | 24.1 | 1.5% |
| Hydrophiidae— 50 | | 34.0 | 30.0 | 36.0 |
| Viperinae — 37 | 29.7 | 70.3 | | |
| Crotalinae — 45 | 6.7 | 93.3 | | |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 16[2] | | 31.3 | 62.5 | 6.3 |
| | | GENERA | | |
| Colubridae —198 | 7.6 | 81.8 | 10.6 | |
| Elapidae — 29 | 10.3 | 75.9 | 13.8 | |
| Hydrophiidae— 16 | | 43.8 | 31.3 | 25.0 |
| Viperinae — 8 | 12.5 | 87.5 | | |
| Crotalinae — 6 | | 100.0 | | |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 1 | | | 100.0 | |

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[1] See Table 51.

[2] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

State I —Class 1 (97–136 ventrals)
State II —Classes 2–6 (*c.* 136–*c.* 217)
State III—Classes 7–10 (217–*c.* 297)
State IV—Classes 11–17 (297–456)

### FAMILIAL RANGES OF VARIATION (Table 52)

Colubridae—This family has States I, II, and III in a sample of 976 species of 198 genera. State I occurs in 82 species and 15 genera, II in 778 species and 162 genera, III in 116 species and 21 genera.

The range of number of ventrals is from 97 (*Duberria variegata*) to 304 (*Calamaria gracillima*). The maximum span is 101 (*Calamaria virgulata*).

Elapidae—This family has all four states in a sample of 137 species of 29 genera. State I occurs in 9 species and 3 genera, II in 93 species and 22 genera, III in 33 species and 4 genera, IV in 2 species.

The range is from 112 (*Rhynchoelaps bertholdi*) to 320 (*Calliophis gracilis*). The maximum span is 77 (*Calliophis melanurus*).

Hydrophiidae—The sea snakes have States II, III, and IV in a sample of 50 species of the 16 genera. State II occurs in 17 species and 7 genera, III in 15 species and 5 genera, IV in 18 species and 4 genera.

The range is from 114 (*Lapemis hardwickii*) to 514 (*Hydrophis fasciatus*). The maximum span is 191 (*Hydrophis fasciatus*).

Viperinae—The true vipers have States I and II in a sample of 37 species of the 8 genera. State I occurs in 11 species and 1 genus, II in 26 species and 7 genera.

The range is from 102 (*Cerastes vipera*) to 205 (*Echis coloratus*). The maximum span is 61 (*Echis carinatus*).

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera. State I occurs in 3 species, II in 42 species and 6 genera.

The range is from 120 (*Agkistrodon nepa*) to 237 (*Trimeresurus flavoviridis*). The maximum span is 50 (*Trimeresurus monticola*).

*Azemiops* has State II, with a range of 170–190 and a span of 21.

*Atractaspis* has States II, III, and IV in a sample of 16 species.

The range is from 177 (*A. battersbyi*) to 370 (*A. reticulata*). The maximum span is 58 (*A. reticulata*).

## Phyletics of Character 20

Character States I and III are rare in the colubrids (table 52) (Criterion 2).

State III, high number of ventrals, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Apostolepis ambinigra*
- *Arizona elegans*
- *Boiga blandingi*
  - *cynodon*
  - *dendrophila*
  - *irregularis*
  - *jaspidea*
  - *kraepelini*
  - *multimaculata*
  - *pulverulentus*
  - *trigonatus*
- *Chilorhinophis carpenteri*
- *Clelia fitzingeri*
- *Coluber hippocrepis*
- *Dasypeltis fasciatus*
  - *inornata*
  - *scabra*
- *Dryocalamus davisoni*
- *Elaphe carinata*
  - *flavirufa*
  - *obsoleta*
  - *radiata*
  - *subocularis*
  - *taeniura*
- *Gonyosoma oxycephalum*
- *Imantodes cenchoa*
- *Mehelya chanleri*
  - *poensis*
- *Miodon gabonensis*
- *Pituophis melanoleucus*
  - *sayi*
- *Rhinobothryum bovalli*
- *Scaphiophis albopunctatus*
- *Siphlophis cervinus*

- *Spalerophis diadema*
- *Stilostoma extenuatum*
- *Telescopus semiannulatus*
- *Trimophodon lamba*
- *Tripanurgos compressus*

- Elapidae
  - *Dendroaspis angusticeps*
    - *jamesoni*
    - *polylepis*
  - *Furina diadema*
  - *Hoplocephalus bungaroides*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Maticora bivirgata*
  - *Micruroides euryxanthus*
  - *Micrurus lemniscatus*
    - *mipartitus*
  - *Ophiophagus hannah*
  - *Oxyuranus scutellatus*
  - *Pseudechis papuanus*
  - *Toxicocalamus stanleyanus*
- Hydrophiidae
  - *Astrotia stokesii*
  - *Enhydrina schistosa*
  - *Hydrophis belcheri*
    - *caerulescens*
    - *inornatus*
    - *major*
    - *ornatus*
    - *torquatus*
  - *Kerilia jerdoni*
  - *Laticauda colubrina*
    - *laticauda*
  - *Microcephalophis gracilis*
  - *Thalassophina viperina*
  - *Thalassophis anomalus*
- *Atractaspis bibroni*
  - *dahomeyensis*
  - *irregularis*
  - *microlepidota*

In these colubrids this character state has a higher frequency of correlation with derived states of 13 other characters compared to the frequency distribution of these states of the same 13 characters in the total sample (table 53) (Criterion 3).

Also, these colubrids have a markedly larger number of species confined to the arboreal habitat (42.5 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent—table 54) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State IV, maximum numbers of ventrals, does not occur in the colubrids (unless one includes a single species of *Atractaspis*). It only occurs in the sea snakes and elapids. We apply the uniqueness criterion (1) to State IV, for its presence is unique to derived stocks.

The taxa that have State IV in our working sample are:

- Elapidae
  - *Ultrocalamus preussi*
- Hydrophiidae
  - *Hydrophis brookii*
    - *cyanocinctus*
    - *fasciatus*
    - *kingi*
    - *klossi*
    - *lapemoides*
    - *mamillaris*
    - *melanocephalus*
    - *melanosoma*
  - *Kolpophis annandalei*
  - *Microcephalophis cantoris*
  - *Pelamis platurus*

TABLE 53. Correlation of States I and III of Character 20 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State I of Character 20 | In species having State III of Character 20 | In total working sample |
| 1 | 45.8% (8)* | | 14.3% (28) |
| 2 | 29.2 (5) | | 15.6 (31) |
| 4 | | 22.5% (1) | 3.8 (4) |
| 5 | 20.8 (9) | | 3.5 (9) |
| 7 | 45.8 (9) | | 25.5 (56) |
| 9 | | 17.5 (7) | 6.8 (14) |
| 11 | | 45.0 (9) | 26.7 (50) |
| 13 | | 50.0 (8) | 31.8 (54) |
| 14 | 17.4 (4) | | 3.5 (7) |
| 16 | | 51.3 (11) | 21.7 (34) |
| 19 | 69.6 (13) | | 36.8 (68) |
| 21 | | 55.0 (11) | 18.9 (29) |
| 22 | 41.7 (8) | 25.0 (7) | 4.5 (11) |
| 26 | | 21.9 (2) | 12.6 (19) |
| 29 | 29.4 (5) | 22.5 (7) | 10.1 (27) |
| 31 | | 46.2 (11) | 19.5 (44) |
| 32 | 52.9 (7) | | 26.3 (55) |
| 38 | 37.5 (6) | | 16.2 (27) |
| 41 | | 20.0 (5) | 10.9 (20) |
| 44 | | 15.6 (4) | 5.8 (11) |
| 46 | | 47.5 (11) | 26.9 (52) |

* Number of genera.

The serial nature of ventrals makes a single trend in the arrangement of these designated states most probable (fig. 19).

Note that compared to the other groups, the sea snakes show much more variability in ventrals as well as greater numbers of scales. This is presumably related to a less firm correlation with vertebral number (Voris, 1969). The situation probably reflects less stringent, or at least different, requirements for locomotion in oceanic than in other conditions (cf. Gans, 1962; Kerfoot, 1970).

TABLE 54. Habitat distribution of colubrid species having States I and III of Character 20 compared to the total colubrid sample.

| | Total Working Sample | State I Character 20 | State III Character 20 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | 8.3 | 42.5 |
| Arboreal | 16.5 | | 42.5 |
| Aquatic | 14.9 | 29.2 | |
| Subterrestrial | 10.8 | 41.7 | 2.5 |
| Fossorial | 12.4 | 16.7 | 12.5 |
| Variation | 5.3 | | |
| Unknown | 3.5 | 4.2 | |

State I, a low number of ventrals, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Amastridium veliferum*
  - *Arrhyton vittatum*
  - *Carphophis amoena*
  - *Chilomeniscus cinctus*
    - *fasciatus*
  - *Coniophanes fissidens*
  - *Conopsis lineatus*
    - *nasus*
  - *Enhydris bocourti*
    - *plumbea*
  - *Haldea striatula*
    - *valeriae*
  - *Helicops angulatus*
    - *leopardinus*
  - *Heterodon simus*
  - *Liodytes alleni*
  - *Macrocalamus lateralis*
  - *Natrix anoscopus*
    - *kirtlandi*
  - *Pseudorabdion collaris*
  - *Rhadinaea decorata*
  - *Storeria occipitomaculata*
  - *Tantilla gracilis*
  - *Trirhinopholis styani*
- Elapidae
  - *Acanthophis antarcticus*
  - *Aspidelaps scutatus*
  - *Brachyaspis curta*
  - *Elapognathus minor*
  - *Rhynchoelaps bertholdi*
- Viperinae
  - *Adenorhinos barbouri*
  - *Atheris hindii*
  - *Bitis atropos*
    - *gabonica*
    - *heraldica*
    - *nasicornis*
  - *Causus defilippii*
    - *lineatus*
    - *rhombeatus*
  - *Cerastes vipera*
  - *Vipera ursini*
- Crotalinae
  - *Agkistrodon nepa*
  - *Bothrops nummifer*
  - *Trimeresurus okinavensis*

In these colubrids character State I has a higher frequency of correlation with derived states of 10 other characters compared to the frequency distribution of these states of the same 10 characters in the total sample (table 53) (Criterion 3).

Also, these colubrids have a markedly larger number of species confined to the aquatic and subterrestrial habitats (29.2 per cent, 41.7 per cent) compared to the relative abundance of aquatic and subterrestrial colubrid species in the total working sample (14.9, 10.8 per cent) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State I probably arose in a different sequential direction from States III and IV because State I correlates mostly with derived states of different characters (table 53) and is predominantly abundant in different habitat zones (table 54).

Our interpretation of the phyletics of Character 20 is shown in Figure 19.

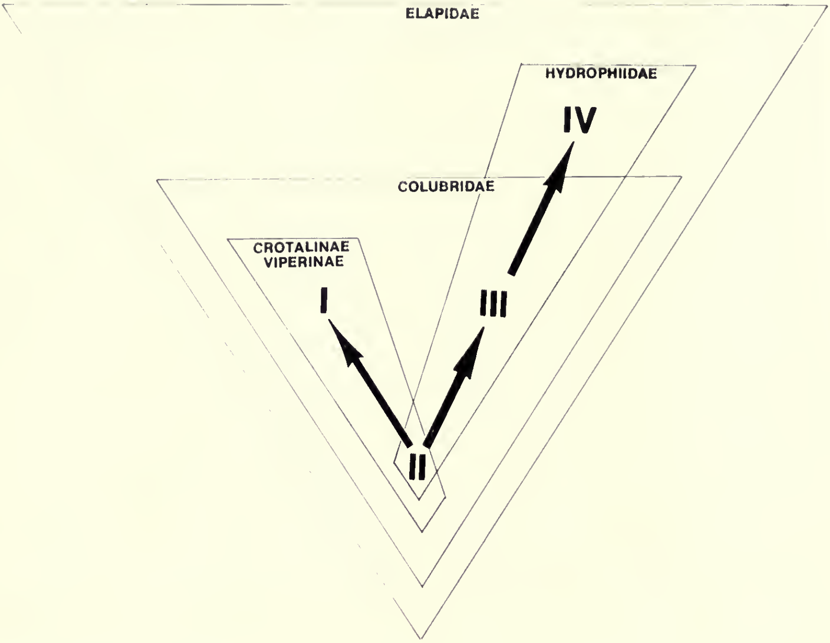

FIG. 19. Distribution among families of states of Character 20. Direction of change among states shown by arrows.

## Character 21—Keeling of Ventral Shields

### DESCRIPTION OF CHARACTER

In some species the ventrals are bent or "keeled" laterally. There are no processes on these scales such as is present on a keeled dorsal scale.

Three states are recognized:

State I —ventrals unkeeled

State II —ventrals keeled—i.e., with a single lateral keel on each side; keels may be strongly raised ("keeled" of Boulenger, 1893–96) or less prominent (*ibid.*)

State III—intraspecific variation; both States I and II present

TABLE 55. Distribution of character states of the ventrals.

| | STATES | | | |
|---|---|---|---|---|
| | I | III | II | |
| Description | Unkeeled | Intraspecific Variation | Keeled | |
| | | SPECIES | | |
| Colubridae[1] —983 | 57.2% | 15.5% | 27.4% | |
| Elapidae[1] —140 | 96.4 | | 3.6 | |
| Hydrophiidae[2] — 41 | 61.0 | 2.4 | 36.6 | |
| Viperinae[3] — 38 | 89.5 | | 10.5 | |
| Crotalinae[3] — 45 | 100.0 | | | |
| *Azemiops*[3] — 1 | 100.0 | | | |
| *Atractaspis*[4] — 16 | 100.0 | | | |
| | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —194 | 70.1 | | 22.7 | 7.2% |
| Elapidae — 30 | 93.3 | | 6.7 | |
| Hydrophiidae — 15 | 66.7 | | 20.0 | 13.3 |
| Viperinae — 8 | 62.5 | | 25.0 | 12.5 |
| Crotalinae — 6 | 100.0 | | | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

## Familial Ranges of Variation (Table 55)

Colubridae—This family has all three states in a sample of 983 species of 194 genera. State I occurs in 562 species of 136 genera, II in 269 species of 44 genera, III in 152 species of 14 genera.

Elapidae—This family has States I and II in a sample of 140 species of 30 genera. State I occurs in 135 species of 28 genera, II in 5 species of 2 genera.

Hydrophiidae—The sea snakes have all three states in a sample of 41 species of 15 genera. The monotypic genus *Acalyptophis* lacks ventral shields and is not included in this sample. State I occurs in 25 species of 11 genera, II in 15 species of 5 genera, III occurs in *Emydocephalus annulatus*.

Intrageneric variation occurs in *Emydocephalus* (II and III) and *Hydrophis* (I and II).

Viperinae—The true vipers have States I and II in a sample of 38 species of the 8 genera. State I occurs in 34 species of 6 genera, II in 4 species of 3 genera.

Intrageneric variation occurs in *Bitis*.

Crotalinae—All the pit vipers have State I in a sample of 45 species of the 6 genera.

*Azemiops* and *Atractaspis* have State I.

## PHYLETICS OF CHARACTER 21

Character State II is not rare in the colubrids (table 55).

State II, keels on the ventrals, occurs in the following 40 colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Boiga blandingi*
    - *cynodon*
    - *dendrophila*
    - *irregularis*
    - *jaspidea*
    - *kraepelini*
    - *multimaculata*
    - *pulverulentus*
    - *trigonatus*
  - *Chrysopelea ornata*
  - *Dromicodryas bernieri*
  - *Elaphe frenata*
    - *radiata*
  - *Gastropyxis smaragdina*
  - *Gonyosoma oxycephalum*
  - *Hapsidophryx lineata*
  - *Holarchus albocinctus*
    - *cyclurus*
    - *formosanus*
    - *hainonensis*
  - *Leptophis mexicanus*
    - *occidentalis*
  - *Lycodon aulicus*
  - *Lystrophis d'orbignyi*
    - *semicinctus*
  - *Lytorhynchus diadema*
  - *Mehelya capensis*
    - *chanleri*
    - *poensis*
  - *Oxyrhabdium modestum*
  - *Philothalmus heterodermus*
    - *irregularis*
  - *Rhamnophis aethiopissa*
  - *Rhinobothryum bovalli*
  - *Simophis rhinostoma*
  - *Siphlophis cervinus*
  - *Stegonotus borneensis*
    - *magnus*
  - *Trimorphodon lambda*
  - *Tripanurgos compressus*
- Elapidae
  - *Hoplocephalus bitorquatus*
    - *bungaroides*
- Hydrophiidae
  - *Aipysurus apraefrontalis*
    - *duboisii*
    - *eydouxi*
    - *foliosquama*
    - *fuscus*
    - *laevis*
  - *Emydocephalus ijimae*
  - *Enhydrina schistosa*
  - *Hydrophis brookii*
    - *fasciatus*
    - *lapemoides*
    - *mamillaris*
    - *melanocephalus*
    - *melanosoma*
  - *Thalassophis anomalus*
- Viperinae
  - *Bitis peringueyi*
  - *Cerastes cerastes*
    - *vipera*
  - *Eristicophis macmahoni*

In these colubrids this character state has a higher frequency of correlation with derived states of eight other characters compared

TABLE 56. Correlation of State II of Character 21 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State II of Character 21 | | In total working sample | |
| 4 | 22.5% | (1)* | 3.8% | (4) |
| 11 | 45.0 | (11) | 26.7 | (50) |
| 13 | 47.5 | (9) | 31.8 | (54) |
| 20 | 55.0 | (12) | 41.2 | (74) |
| 26 | 32.3 | (5) | 12.6 | (19) |
| 31 | 37.8 | (7) | 19.5 | (44) |
| 33 | 61.5 | (11) | 43.0 | (76) |
| 43 | 10.0 | (2) | 1.9 | (3) |

* Number of genera.

TABLE 57. Habitat distribution of colubrid species having State II of Character 21 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 21 % |
|---|---|---|
| Terrestrial | 36.2 | 45.0 |
| Arboreal | 16.5 | 40.0 |
| Aquatic | 14.9 | |
| Subterrestrial | 10.8 | 2.5 |
| Fossorial | 12.4 | 5.0 |
| Variation | 5.3 | 5.0 |
| Unknown | 3.5 | 2.5 |

to the frequency distribution of these states of the same eight characters in the total sample (table 56) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the arboreal habitat (40.0 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent) (table 57) (Criterion 5).

Also, a substantially greater proportion of these colubrid species come from the Old World (77.5 per cent) compared to the relative abundance of colubrids from the same area (44.6 per cent) in the total working sample (Criterion 6). This preponderant Old World distribution is also true for all the colubrid species having intraspecific variation (State III).

The application of three criteria (3, 5, 6) suggests that State II is derived (Criterion 8).

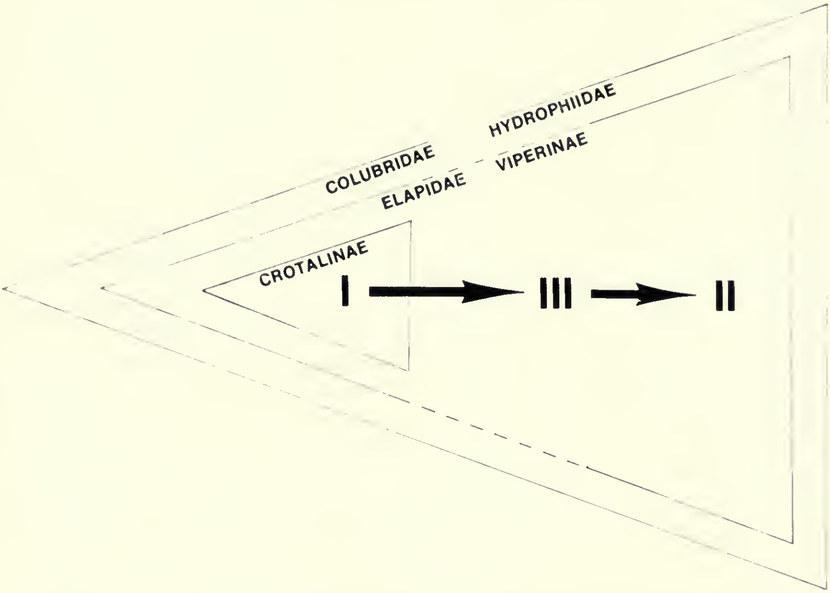

FIG. 20. Distribution among families of states of Character 21. Direction of change among states shown by arrows.

State III is found in the following taxa:

Colubridae
- *Coluber florulentus*
  - *gemonensis*
  - *hippocrepis*
  - *jugularis*
  - *najadum*
  - *rhodorhachis*
  - *spinalis*
  - *ventromaculatus*
- *Dispholidus typus*
- *Dryocalamus davisoni*
- *Elaphe dione*
  - *taeniura*
- *Lioheterodon madagascariensis*
- *Ptyas korros*
  - *mucosus*
- *Spalerosophis diadema*
- *Thrasops flavigularis*

Hydrophiidae
- *Emydocephalus annulatus*

State III is an intermediate sequential state because each taxon with this state has both States I and II.

Our interpretation of the phyletics of Character 21 is shown in Figure 20.

## Character 22—Number of Subcaudals

### DESCRIPTION OF CHARACTER

Subcaudals are the enlarged paired or single plates on the ventral side of the tail. Their count is from the vent to the terminal caudal scute. See Peters (1964, p. 340) for a description of this character.

### CLASSES AND STATES

The total range of variation in number of subcaudals is segmented by steps of 30, since a span of 30 covers most of the intraspecific variation encountered (91.3 per cent—table 58).

Four characters used in this study (11, 16, 20, 22) only have ranges given for each taxon (literature cited in table 58). Therefore means of each taxon could not be determined from the literature. Our method of assigning taxa to a range is explained under Character 11. Thirteen classes were delimited (table 59) and four states are recognized:

State I —Classes 2–8 (*c.* 35–*c.* 126 subcaudals)
State II —Classes 9–10 (126—*c.* 156)
State III—Classes 11–13 (156—215)
State IV—Class 1 (6–35)

### FAMILIAL RANGES OF VARIATION (Table 60)

Colubridae—This family has all four states in a sample of 962 species of 195 genera. State I occurs in 715 species and 143 genera, II in 70 species and 19 genera, III in 14 species, IV in 163 species and 33 genera.

The range of the number of subcaudals is from 6 (*Calamaria septentrionalis*) to 208 (*Lycodon albofuscus*). The maximum span is 81 (*Liopholidophis sexlineatus*).

Elapidae—This family has States I and IV in a sample of 135 species of 28 genera. State I occurs in 59 species and 19 genera, IV in 76 species and 9 genera.

The range of the number of subcaudals is from 12 (*Leptomicrurus collaris*) to 121 (*Dendroaspis angusticeps* and *D. jamesoni*). The maximum span is 38 (*Ophiophagus hannah*).

Hydrophiidae—The sea snakes have States I and IV in a sample of 13 species of 3 genera. State I occurs in 5 species and one genus, IV in 8 species and 2 genera.

The range of the number of subcaudals is from 19 (*Aipysurus apraefrontalis*) to 47 (*Laticauda colubrina* and *L. laticauda*). The maximum span is 19 (*Laticauda colubrina*).

TABLE 58. Spans in number of subcaudals by species and families.

| | | Number of Species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae[1] | Elapidae[1] | Hydrophiidae[2] | Viperinae[3,4] | Crotalinae[3] |
| 1 | 223 | 197 | 24 | 1 | | 1 |
| 2 | 15 | 9 | 5 | | | 1 |
| 3 | 25 | 17 | 4 | | 2 | 2 |
| 4 | 14 | 9 | 2 | 1 | 2 | |
| 5 | 27 | 22 | 5 | | | |
| 6 | 38 | 30 | 6 | | | 2 |
| 7 | 29 | 23 | 4 | 1 | 1 | |
| 8 | 34 | 22 | 8 | 1 | 1 | 2 |
| 9 | 50 | 38 | 6 | 1 | 4 | 1 |
| 10 | 48 | 37 | 4 | 3 | 3 | 1 |
| 11 | 45 | 30 | 11 | 1 | 2 | 1 |
| 12 | 43 | 28 | 9 | 1 | 4 | 1 |
| 13 | 45 | 34 | 6 | | 1 | 4 |
| 14 | 43 | 29 | 4 | 2 | 3 | 5 |
| 15 | 51 | 42 | 4 | | 2 | 3 |
| 16 | 37 | 29 | 5 | | | 3 |
| 17 | 30 | 21 | 6 | | 2 | 1 |
| 18 | 38 | 28 | 4 | | 3 | 3 |
| 19 | 40 | 30 | 4 | 1 | 1 | 4 |
| 20 | 24 | 20 | 3 | | 1 | |
| 21 | 33 | 29 | 1 | | 1 | 2 |
| 22 | 21 | 17 | | | 2 | 2 |
| 23 | 24 | 18 | 4 | | 2 | |
| 24 | 19 | 18 | | | | 1 |
| 25 | 15 | 13 | | | | 2 |
| 26 | 19 | 18 | | | | 1 |
| 27 | 17 | 17 | | | | |
| 28 | 18 | 15 | 1 | | 1 | 1 |
| 29 | 13 | 13 | | | | |
| 30 | 10 | 9 | 1 | | | |
| 31 | 14 | 14 | | | | |
| 32 | 11 | 11 | | | | |
| 33 | 8 | 8 | | | | |
| 34 | 5 | 4 | 1 | | | |
| 35 | 5 | 5 | | | | |
| 36–40 | 22 | 20 | 2 | | | |
| 41–45 | 18 | 17 | | | | 1 |
| 46–47 | 3 | 3 | | | | |
| 49–55 | 10 | 10 | | | | |
| 57–58 | 4 | 4 | | | | |
| 60 | 1 | 1 | | | | |
| 64 | 1 | 1 | | | | |
| 81 | 1 | 1 | | | | |
| Total | 1,192 | 962 | 134 | 13 | 38 | 45 |
| Span 30 or less | 91.3% | 89.6% | 97.8% | 100.0% | 100.0% | 97.8% |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926, 1931.

[3] Working sample.

[4] Excluding *Azemiops* and *Atractaspis*.

TABLE 59. Frequency distribution of species in range classes of number of subcaudals in families of advanced snakes.

| Class | Range | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 6–35 | 163/33 | 59/9 | 8/2 | 21/5 | 16/2 |
| 2 | Intermediate[2] | 29/12 | 9/6 | 2/1 | 3/2 | 4/0 |
| 3 | 36–65 | 250/48 | 52/8 | 3/0 | 14/1 | 19/3 |
| 4 | Intermediate | 66/19 | 2/1 | | | 2/1 |
| 5 | 66–95 | 215/34 | 8/3 | | | 4/0 |
| 6 | Intermediate | 28/10 | 1/0 | | | |
| 7 | 96–125 | 103/14 | 4/1 | | | |
| 8 | Intermediate | 24/6 | | | | |
| 9 | 126–155 | 57/15 | | | | |
| 10 | Intermediate | 13/4 | | | | |
| 11 | 156–185 | 8/0 | | | | |
| 12 | Intermediate | 3/0 | | | | |
| 13 | 186–215 | 3/0 | | | | |
| Totals | | 962/195 | 135/28 | 13/3 | 38/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] See Character 11 text for explanation.

TABLE 60. Distribution of character states of the number of subcaudals.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Classes[1] | 2–8 | 9–10 | 11–13 | 1 |
| | SPECIES | | | |
| Colubridae —962 | 74.3% | 7.3% | 1.5% | 16.9% |
| Elapidae —135 | 56.3 | | | 43.7 |
| Hydrophiidae— 13 | 38.5 | | | 61.5 |
| Viperinae — 38 | 44.7 | | | 55.3 |
| Crotalinae — 45 | 64.4 | | | 35.6 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 16[2] | 6.3 | | | 93.8 |
| | GENERA | | | |
| Colubridae —195 | 73.3 | 9.7 | | 16.9 |
| Elapidae — 28 | 67.9 | | | 32.1 |
| Hydrophiidae— 3 | 33.3 | | | 66.7 |
| Viperinae — 8 | 37.5 | | | 62.5 |
| Crotalinae — 6 | 66.7 | | | 33.3 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | | | | 100.0 |

[1] See Table 59.

[2] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Viperinae—The true vipers have States I and IV in a sample of 38 species of the 8 genera. State I occurs in 17 species and 3 genera, IV in 21 species and 5 genera.

The range of the number of subcaudals is from 10 (*Causus defilippii*) to 65 (*Atheris squamiger*). The maximum span is 28 (*Echis carinatus*).

Crotalinae—The pit vipers have States I and IV in a sample of 45 species of the 6 genera. State I occurs in 29 species and 4 genera, IV in 16 species and 2 genera.

The range of the number of subcaudals is from 13 (*Crotalus horridus*) to 96 (*Trimeresurus mucrosquamatus*). The maximum span is 41 (*Trimeresurus monticola*).

*Azemiops* has State I.

*Atractaspis* has States I and IV in a sample of 16 species. The range of number of subcaudals is from 16 (*A. bibroni*) to 39 (*A. engaddensis*).

### PHYLETICS OF CHARACTER 22

Character States II, III, and IV are rare in the colubrids (table 60) (Criterion 2).

State II, a large number of subcaudals, occurs only in the following colubrids in our working sample:

Colubridae
- *Alsophis portoreicensis*
  - *sanctae-crucis*
- *Boiga blandingi*
  - *cynodon*
  - *jaspidea*
  - *kraepelini*
- *Chironius carinatus*
- *Coluber rhodorhachis*
- *Gastropyxis smaragdina*
- *Gonyosoma oxycephalum*
- *Imantodes conchoa*
- *Leptophis mexicanus*
  - *occidentalis*
- *Masticophis schotti*
- *Oxybelis argenteus*
- *Passerita mycterizans*
  - *nasuta*
- *Pseustes poecilonotus*
  - *sulphureus*
- *Ptyas korros*
- *Rhamnophis aethiopissa*
- *Salvadora lemniscata*
  - *mexicana*
- *Thelotornis kirtlandii*
- *Thrasops flavigularis*
- *Zaocys nigromarginatus*

In these colubrids this character state has a higher frequency of correlation with derived states of five other characters compared to the frequency distribution of these states of the same five characters in the total working sample (table 61) (Criterion 3).

Also, these colubrids have a markedly larger number of species confined to the arboreal habitat (53.8 per cent) compared to the relative abundance of arboreal colubrid species in the total working sample (16.5 per cent—table 62) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State III, maximal numbers of subcaudals (table 59), only occurs in the following colubrids in our working sample:

Colubridae
- *Oxybelis aeneus*
  - *brevirostris*
  - *fulgidus*
- *Passerita prasinus*
- *Uromacer catesbyi*
  - *oxyrhynchus*

All these species are arboreal (Criterion 5).

The application of two criteria (2, 5) suggests this state is derived.

The serial nature of subcaudals makes a single trend in the arrangement of these designated states most probable (fig. 21). This is further emphasized for snakes with these states (II, III) are predominantly abundant in the same habitat zone.

State IV, low number of subcaudals, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Apostolepis ambinigra*
  - *Aspidura trachyprocta*
  - *Atractus elaps*
    - *erythromelas*
    - *ventrimaculatus*
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Carphophis amoena*
  - *Chilomeniscus cinctus*
    - *fasciatus*
  - *Chilorhinophis carpenteri*
  - *Conopsis lineatus*
    - *nasus*
  - *Drepanoides eatonii*
  - *Geophis semidoliatus*
  - *Haldea valeriae*
  - *Macrocalamus lateralis*
  - *Miodon gabonensis*
  - *Phyllorhynchus decurtatus*
  - *Prosymna ambigua*
  - *Pseudorabdion collaris*
  - *Tantilla gracilis*
  - *Trirhinopholis styani*
  - *Tropidocloniom lineatum*
- Elapidae
  - *Apistocalamus lonnbergi*
  - *Aspidelaps lubricus*
    - *scutatus*
  - *Aspidomorphus muelleri*
  - *Brachyaspis curta*
  - *Brachyurophis semifasciata*
  - *Bungarus fasciatus*
  - *Cacophis harriettae*
  - *Calliophis japonicus*
  - *Denisonia fasciata*
  - *Elapsoidea sundevalli*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Micropechis elapsoides*
  - *Micruroides euryxanthus*
  - *Micrurus mipartitus*
    - *spixi*
  - *Ogmodon vitianus*
  - *Parapistocalamus hedigeri*
  - *Rhynchoelaps bertholdi*
  - *Vermicella annulata*
- Hydrophiidae
  - *Aipysurus*
  - *Emydocephalus*
- Viperinae
  - *Adenorhinos*
  - *Atheris hindii*
  - *Bitis*
  - *Causus*
  - *Cerastes vipera*
  - *Eristicophis*
  - *Vipera ammodytes*
    - *ursini*
    - *xanthina*
- Crotalinae
  - *Bothrops godmani*
    - *nummifer*
  - *Crotalus*
  - *Sistrurus*
- *Atractaspis bibroni*
  - *corpulenta*
  - *dahomeyensis*
  - *irregularis*
  - *microlepidota*

In these colubrids this character state has a higher frequency of correlation with derived states of 18 other characters compared to the frequency distribution of these states of the same 18 characters in the total sample (table 61) (Criterion 3).

Also, these colubrids have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—92.9 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (table 62) (Criterion 5).

TABLE 61. Correlation of States II and IV of Character 22 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 22 | In species having State IV of Character 22 | In total working sample |
| 1 | | 42.9% (8) | 14.3% (28) |
| 2 | | 35.7 (8) | 15.6 (31) |
| 5 | | 25.0 (6) | 3.5 (9) |
| 7 | | 78.6 (15) | 25.5 (56) |
| 9 | | 28.6 (5) | 6.8 (14) |
| 11 | 48.0% (9)* | | 26.7 (50) |
| 13 | 69.2 (12) | | 31.8 (54) |
| 19 | | 77.8 (16) | 36.8 (68) |
| 21 | 50.0 (8) | | 18.9 (29) |
| 26 | 28.6 (4) | | 12.6 (19) |
| 28 | | 47.4 (6) | 11.7 (26) |
| 29 | | 38.1 (8) | 10.1 (27) |
| 32 | | 71.4 (11) | 26.3 (55) |
| 33 | 61.5 (10) | | 43.0 (76) |
| 34 | | 40.9 (9) | 6.8 (18) |
| 35 | | 15.4 (4) | 2.0 (6) |
| 36 | | 25.9 (7) | 6.1 (16) |
| 38 | | 47.4 (8) | 16.2 (27) |
| 40 | | 53.6 (13) | 24.8 (54) |
| 42 | | 40.0 (7) | 8.7 (14) |
| 47 | | 67.9 (12) | 48.5 (84) |
| 49 | | 27.3 (6) | 15.5 (26) |
| 50 | | 45.8 (7) | 20.0 (24) |

* Number of genera.

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State IV probably arose in a different sequential direction from States II and III because State IV correlates with derived states of different character (table 61) and is predominantly more abundant in different habitat zones (table 62).

TABLE 62. Habitat distribution of colubrid species having States II and IV of Character 22 compared to the total colubrid working sample.

| | Total Working Sample | STATES | |
|---|---|---|---|
| | | II | IV |
| Terrestrial | 36.2% | 26.9% | 3.6% |
| Arboreal | 16.5 | 53.8 | |
| Aquatic | 14.9 | | |
| Subterrestrial | 10.8 | | 28.6 |
| Fossorial | 12.4 | | 64.3 |
| Variation | 5.3 | 19.2 | |
| Unknown | 3.5 | | 3.6 |

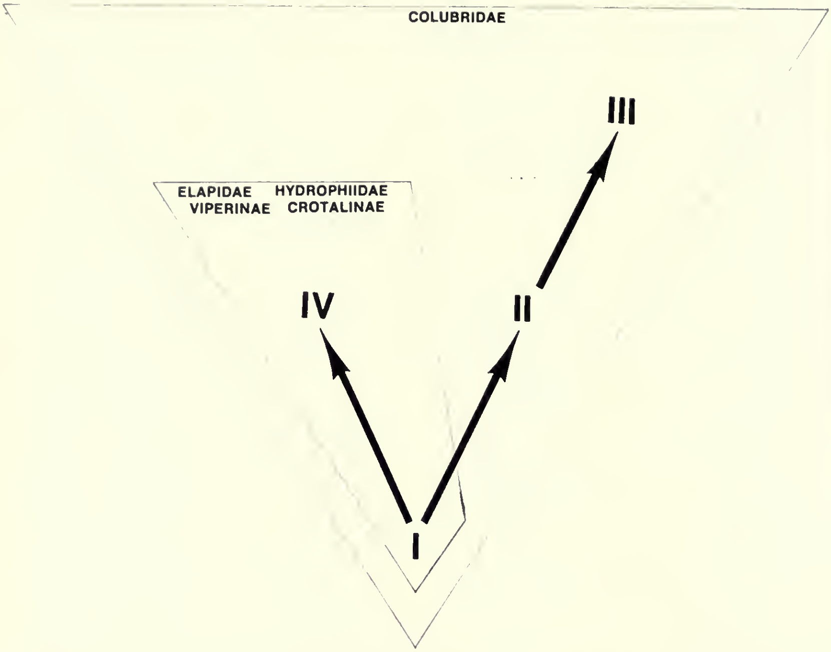

Fig. 21. Distribution among families of states of Character 22. Direction of change among states shown by arrows.

Our interpretation of the phyletics of Character 22 is shown in Figure 21.

### Character 23—Keeling of Subcaudal Shields

#### Description of Character

The subcaudal shields are sometimes bent or angled laterally. As with the ventrals, three states are recognized:

State I —subcaudals unkeeled

State II —intraspecific variation, both States I and III present

State III—subcaudals keeled—i.e., with a single lateral keel on each side

#### Familial Ranges of Variation (Table 63)

Colubridae—This family has States I and III in a sample of 1,001 species of 199 genera. State I occurs in 965 species of 190 genera, III in 36 species of 9 genera.

TABLE 63. Distribution of character states of subcaudals.

| | | STATES | | | |
|---|---|---|---|---|---|
| | | I | II | III | |
| Description | | Unkeeled | Intraspecific Variation | Keeled | |
| | | | SPECIES | | |
| Colubridae[1] | —1001 | 96.4% | | 3.6% | |
| Elapidae[1] | — 143 | 100.0 | | | |
| Hydrophiidae[2] | — 12 | 100.0 | | | |
| Viperinae[3] | — 38 | 86.8 | 2.6% | 10.5 | |
| Crotalinae[3] | — 45 | 100.0 | | | |
| *Azemiops*[3] | — 1 | 100.0 | | | |
| *Atractaspis*[4] | — 16 | 100.0 | | | |
| | | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae | — 199 | 95.5 | | 4.5 | |
| Elapidae | — 30 | 100.0 | | | |
| Hydrophiidae | — 3 | 100.0 | | | |
| Viperinae | — 8 | 75.0 | | 12.5 | 12.5 |
| Crotalinae | — 6 | 100.0 | | | |
| *Azemiops* | — 1 | 100.0 | | | |
| *Atractaspis* | — 1 | 100.0 | | | |

[1] Boulenger, 1893–96.
[2] M. A. Smith, 1926, 1931.
[3] Working sample.
[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

Elapidae, Crotalinae—All taxa of these two groups have State I in a sample of 188 species (143, 45) of 36 genera (30, 6).

Hydrophiidae—The sea snakes have subcaudals in 12 species of 3 genera, all of which have State I. The remaining taxa (30 species, 13 genera) all lack subcaudal shields and are not included in this sample.

Viperinae—The true vipers have all three states in a sample of 38 species of the 8 genera. State I occurs in 33 species of 7 genera, II in *Bitis arietans*, III in 4 species of 2 genera. Intrageneric variation occurs in *Bitis*, which has all 3 states.

*Azemiops* and *Atractaspis* have State I.

## PHYLETICS OF CHARACTER 23

State III is rare in the colubrids (table 63) (Criterion 2).

State III, keeled subcaudals, occurs in the following colubrids (plus other taxa) in our working sample:

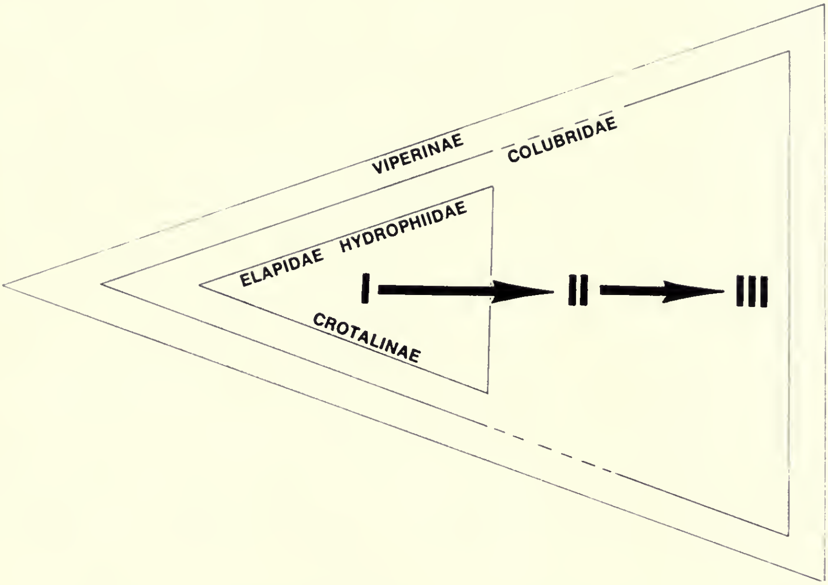

FIG. 22. Distribution among families of states of Character 23. Direction of change among states shown by arrows.

Colubridae
  *Chrysopelea ornata*
  *Gastropyxis smaragdina*
  *Philothalmus heterodermus*
    *irregularis*

Viperinae
  *Bitis cornutus*
    *peringueyi*
  *Cerastes cerastes*
    *vipera*

These colubrids are all arboreal or partly arboreal (Criterion 5). They also are all from the Old World (as are those three species with intraspecific variation (see below) (Criterion 6).

The application of three criteria (2, 5, 6) suggests that this state is derived (Criterion 8).

State II is also very rare in colubrids. The two colubrids and the single viper having intraspecific variation in our working sample are:

*Oxyrhabdium modestum*
*Spalerosophis diadema*
*Bitis arietans*

State II is an intermediate sequential state because each taxon with this state has both States I and III.

Our interpretation of the phyletics of Character 23 is shown in Figure 22.

## Character 24—Subcaudals Paired or Single

### DESCRIPTION OF CHARACTER

The subcaudal scales may consist of one or two rows of scales spanning the ventral side of the tail. In some specimens both conditions occur.

Three states are recognized:

State I —subcaudals paired
State II —intraspecific variation, both States I and III present (Marx, 1953, fig. 40A)
State III—subcaudals single

### FAMILIAL RANGES OF VARIATION (Table 64)

Colubridae—This family has all three states in a sample of 987 species of 196 genera. State I occurs in 944 species of 170 genera,

TABLE 64. Distribution of character states of the subcaudals.

| | | STATES | | |
|---|---|---|---|---|
| | I | II | III | |
| Description | Paired | Intraspecific Variation | Single | |
| | | SPECIES | | |
| Colubridae[1] —987 | 95.6% | 0.3% | 4.1% | |
| Elapidae[1] —116 | 65.5 | 8.6 | 25.9 | |
| Hydrophiidae[2]— 5 | 80.0 | | 20.0 | |
| Viperinae[3] — 38 | 81.6 | | 18.4 | |
| Crotalinae[3] — 45 | 44.4 | 31.1 | 24.4 | |
| *Azemiops*[3] — 1 | 100.0 | | | |
| *Atractaspis*[4] — 16 | 25.0 | 50.0 | 25.0 | |
| | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —196 | 86.7 | 6.1 | 7.1 | |
| Elapidae — 28 | 53.6 | 25.0 | 21.4 | |
| Hydrophiidae — 2 | 50.0 | | 50.0 | |
| Viperinae — 8 | 37.5 | | 25.0 | 37.5% |
| Crotalinae — 6 | 16.7 | | | 83.3 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | | | | 100.0 |

[1] Boulenger, 1893–96.

[2] M. A. Smith, 1926.

[3] Working sample.

[4] Parker, 1949; Haas, 1950; Laurent, 1950; de Witte, 1959; Perret, 1960.

II in 3 species, III in 40 species of 14 genera. Intrageneric variation occurs in 12 genera.

Elapidae—This family has all three states in a sample of 116 species of 28 genera. State I occurs in 76 species of 15 genera, II in 10 species, III in 30 species of 6 genera. Intrageneric variation occurs in 7 genera.

Hydrophiidae—The sea snakes have States I and III in a sample of 5 species of 2 genera. State I occurs in 4 species of *Laticauda,* III occurs in *Emydocephalus ijima.* The remaining taxa all lack subcaudal shields and are not included in this sample.

Viperinae—The true vipers have States I and III in a sample of 38 species of the 8 genera. State I occurs in 31 species of 6 genera, III in 7 species of 5 genera. Intrageneric variation occurs in 3 genera.

Crotalinae—The pit vipers have all three states in a sample of 45 species of the 6 genera. State I occurs in 20 species of 3 genera, II in 14 species of 5 genera, III in 11 species of 2 genera. Intrageneric variation occurs in 3 genera.

*Azemiops* has State I. *Atractaspis* has all three states.

### Phyletics of Character 24

State III is rare in the colubrids (table 64) (Criterion 2).

State III, single subcaudals, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Achalinus spinalis*
  - *Aparallactus lunulatus*
    - *werneri*
  - *Aspidura trachyprocta*
  - *Dipsadoboa unicolor*
  - *Holuropholis olivaceus*
  - *Pythonodipsas carinata*
  - *Rhinocheilus lecontei*
- Elapidae
  - *Brachyaspis curta*
  - *Bungarus candidus*
    - *fasciatus*
    - *multicinctus*
  - *Denisonia coronoides*
    - *fasciata*
    - *nigrescens*
    - *par*
    - *superba*
  - *Elapognathus minor*
  - *Hoplocephalus bitorquatus*
    - *bungaroides*
  - *Notechis scutatus*
- Hydrophiidae
  - *Emydocephalus ijimae*
- Viperinae
  - *Adenorhinos barbouri*
  - *Atheris ceratophorus*
    - *chlorechis*
    - *hispidus*
    - *katangensis*
    - *nitschei*
    - *squamiger*
  - *Bitis worthingtoni*
  - *Causus lichtensteini*
  - *Echis carinatus*
    - *coloratus*

Crotalinae
*Bothrops dunni*
*godmani*
*lansbergi*
*schlegeli*
*Crotalus adamanteus*
*atrox*
*cerastes*
*mitchellii*
*pusillus*
*ruber*
*viridis*
*Atractaspis microlepedota*

In these colubrids this character state has a higher frequency of correlation with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total sample (table 65) (Criterion 3).

TABLE 65. Correlation of State III of Character 24 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State III of Character 24 | | In total working sample | |
| 7 | 75.0% | (5)* | 25.5% | (56) |
| 13 | 50.0 | (3) | 31.8 | (54) |
| 20 | 62.5 | (5) | 41.2 | (74) |
| 28 | 50.0 | (3) | 11.7 | (26) |
| 31 | 57.1 | (4) | 19.5 | (44) |
| 32 | 60.0 | (3) | 26.3 | (55) |
| 36 | 42.9 | (3) | 6.1 | (16) |
| 40 | 50.0 | (4) | 24.8 | (54) |
| 46 | 50.0 | (3) | 27.8 | (52) |

* Number of genera

Also seven of the eight species are from the Old World (Criterion 6).

The application of three criteria (2, 3, 6) suggests that this state is derived (Criterion 8).

The colubrids (plus other taxa) having State II in our working sample are:

Colubridae
*Elaphe mandarina*
*Lioheterodon madagascariensis*
*Rhinobothryum bovalli*
*Scaphiophis albopunctata*
Elapidae
*Acanthophis antarcticus*
*Demansia textilis*
*Leptomicrurus collaris*
*Micrurus affinis*
*mipartitus*
sp.
*spixi*
*Ophiophagus hannah*
*Pseudechis australis*
*papuanus*
*porphyriacus*
*Walterinnesia aegyptia*

Crotalinae
  *Agkistrodon acutus*
    *bilineatus*
    *contortrix*
    *hypnale*
    *piscivorus*
  *Bothrops nummifer*
  *Crotalus basiliscus*
    *durissus*
    *horridus*
    *lepidus*
    *molossus*
  *Lachesis mutus*
  *Sistrurus cateniatus*
    *miliarius*
*Atractaspis bibroni*
    *corpulenta*
    *dahomeyensis*

State II is an intermediate sequential state because each taxon with this state has both states, I and III.

Our interpretation of the phyletics of Character 24 is shown in Figure 23.

## Character 25—Relative Length of Anterior Portion of Skull

### Description of Character

The relative length of the anterior portion of the skull is here defined as the percentage of the total length of the skull that is formed by the distance from the anterior tip of the premaxilla to the

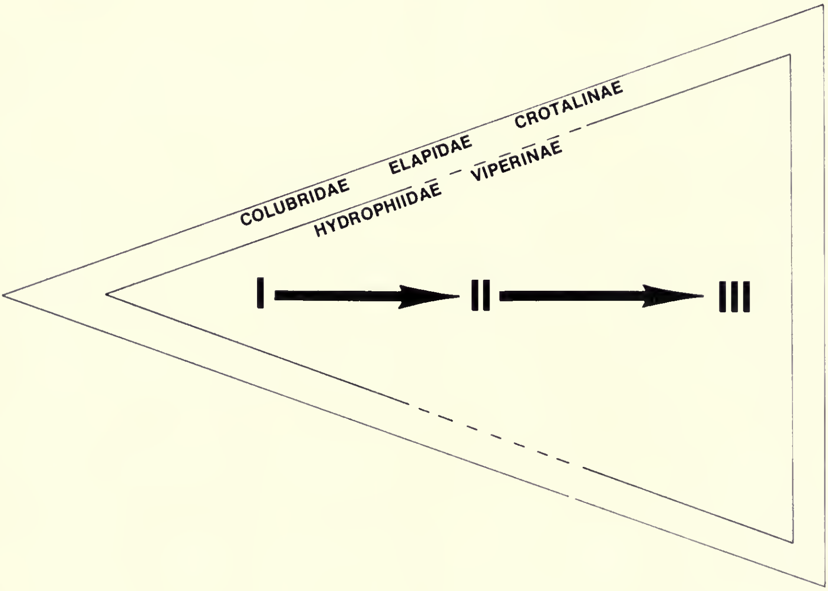

Fig. 23. Distribution among families of states of Character 24. Direction of change among states shown by arrows.

TABLE 66. Frequency distribution of species in range classes of relative length of the anterior portion of the skull in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 38.7–42.6 | 3/2 | 3/3 | | 1/1 | |
| 2 | 42.7–46.6 | 18/11 | 6/4 | 6/2 | 9/1 | 4/0 |
| 3 | 46.7–50.6 | 54/34 | 10/9 | 10/4 | 13/5 | 14/3 |
| 4 | 50.7–54.6 | 76/36 | 9/6 | 10/4 | 8/0 | 17/3 |
| 5 | 54.7–58.6 | 65/28 | 4/3 | 2/0 | 3/1 | 3/0 |
| 6 | 58.7–62.6 | 10/6 | | | | |
| 7 | 62.7–66.6 | 1/1 | | | | |
| Totals | | 227/118 | 32/25 | 28/10 | 34/8 | 38/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

middle of the dorsal frontal-parietal suture. The total length of the skull was measured from the anterior tip of the premaxilla to the midpoint of the dorsal margin of the foramen magnum.

Relative growth effects are to be expected to affect the precision of proportions in characterizing taxa. However, the sample used here was predominantly of the adult age classes and thus variation from this source is minimal. In those cases where young specimens were measured, large adults were almost invariably also available and the resulting averages probably fairly characterize the species.

The remarkable feature of this character is the close proximity of the frontal-parietal suture to the mid-line (table 66) in all familial level taxa. Snakes that span all ecological and zoogeographic zones maintain the fronto-parietal suture almost at the numerical midpoint. This suture therefore was subsequently used as the reference point in measuring skull width (Character 26) and considered in the fang length discussion (Character 45).

### CLASSES AND STATES

The total range of variation in relative length of anterior portion of the skull was segmented by steps of 4.0 per cent, since a span of 4.0 per cent covered most of the intraspecific variation encountered (87.7 per cent—table 67). Seven classes resulted as shown in Table 66. The mean of each taxon was assigned to a class (table 66). States are established when there is a marked change in frequency of number of species between classes.

Three states are recognized:

State I —Classes 3–5 (46.7–58.6 per cent)
State II —Classes 1–2 (38.7–46.6)
State III—Classes 6–7 (58.7–66.6)

### FAMILIAL RANGES OF VARIATION (Table 68)

Colubridae—This family has all three states in a sample from 379 skulls of 227 species of 118 genera. State I occurs in 195 species and 98 genera, II in 21 species and 13 genera, III in 11 species and 7 genera.

The range of variation in the relative length of the anterior portion of the skull is from 41.6 per cent (*Diadophis regalis*) to 65.1 per cent (*Oxybelis fulgidus*). The maximum span in a single species is 17.6 per cent (*Tantilla gracilis*). However, 89.9 per cent of the species have a span of 4.0 per cent or less.

TABLE 67. Spans in relative length of anterior portion of skull by species and families.

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 231 | 150 | 22 | 16 | 16 | 27 |
| 2 | 2 | 2 |  |  |  |  |
| 3 | 2 | 1 | 1 |  |  |  |
| 4 | 2 | 1 |  |  |  | 1 |
| 5 | 4 | 2 |  |  | 1 | 1 |
| 6 | 1 | 1 |  |  |  |  |
| 7 | 2 | 2 |  |  |  |  |
| 8 | 1 | 1 |  |  |  |  |
| 9 | 3 | 1 | 1 |  |  | 1 |
| 10 | 1 | 1 |  |  |  |  |
| 11 | 2 | 2 |  |  |  |  |
| 12 | 2 | 1 | 1 |  |  |  |
| 13 | 3 | 3 |  |  |  |  |
| 14 | 3 | 2 |  |  | 1 |  |
| 15 | 2 | 1 |  |  | 1 |  |
| 16 | 3 | 3 |  |  |  |  |
| 17 | 3 | 2 |  | 1 |  |  |
| 18 | 2 | 1 |  |  | 1 |  |
| 20 | 1 |  |  | 1 |  |  |
| 21–30 | 23 | 13 | 3 | 2 | 2 | 3 |
| 31–40 | 20 | 14 | 1 | 2 | 1 | 2 |
| 41–50 | 19 | 10 | 1 | 2 | 4 | 2 |
| 51–60 | 13 | 7 | 1 | 1 | 4 |  |
| 61–70 | 3 | 2 |  | 1 |  |  |
| 71–80 | 3 | 1 |  | 1 | 1 |  |
| 81–90 | 1 |  |  |  | 1 |  |
| 91–100 | 2 | 2 |  |  |  |  |
| 112 | 1 |  |  |  | 1 |  |
| 133 | 1 |  | 1 |  |  |  |
| 176 | 1 | 1 |  |  |  |  |
| Totals | 357 | 227 | 32 | 27 | 34 | 37 |
| Span 4.0% or less | 87.7% | 89.9% | 90.6% | 81.5% | 67.6% | 94.6% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 68. Distribution of character states of the relative length of the anterior portion of the skull.

| | | STATES | |
|---|---|---|---|
| | II | I | III |
| Classes[1] | 1–2 | 3–5 | 6–7 |
| | | SPECIES | |
| Colubridae —227 | 9.3% | 85.9% | 4.8% |
| Elapidae — 32 | 28.1 | 71.9 | |
| Hydrophiidae— 28 | 21.4 | 78.6 | |
| Viperinae — 34 | 29.4 | 70.6 | |
| Crotalinae — 38 | 10.5 | 89.5 | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 4 | | 100.0 | |
| | | GENERA | |
| Colubridae —118 | 11.0 | 83.1 | 5.9 |
| Elapidae — 25 | 28.0 | 72.0 | |
| Hydrophiidae— 10 | 20.0 | 80.0 | |
| Viperinae — 8 | 25.0 | 75.0 | |
| Crotalinae — 6 | | 100.0 | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | | 100.0 | |

[1] See Table 66.

Elapidae—This family has States I and II in a sample from 51 skulls of 32 species of 25 genera. State I occurs in 23 species and 18 genera, II in 9 species and 7 genera.

The range of variation in the relative length of the anterior portion of the skull is from 40.2 per cent (*Rhynchoelaps bertholdi*) to 59.1 per cent (*Notechis scutatus*). The maximum span in a single species is 13.3 per cent (*Notechis scutatus*). However, 90.6 per cent of the species have a span of 4.0 per cent or less.

Hydrophiidae—The sea snakes have States I and II in a sample from 66 skulls of 28 species of 10 genera. State I occurs in 22 species and 8 genera, II in 6 species and 2 genera.

The range of variation in the relative length of the anterior portion of the skull is from 42.1 per cent (*Laticauda laticaudata*) to 55.9 per cent (*Aipysurus fuscus, Laticauda semifasciata*). The maximum span in a single species is 8.0 per cent (*Laticauda laticaudata*). However, 81.5 per cent of the species have a span of 4.0 per cent or less.

Viperinae—The true vipers have States I and II in a sample from 83 skulls of 34 species of the 8 genera. State I occurs in 24 species and 6 genera, II in 10 species and 2 genera.

The range of variation in the relative length of the anterior portion of the skull is from 38.7 per cent (*Adenorhinos barbouri*) to 62.8 per cent (*Causus rhombeatus*). The maximum span in a single species is 11.2 per cent (*Causus rhombeatus*). However, 67.6 per cent of the species have a span of 4.0 per cent or less.

Crotalinae—The pit vipers have States I and II in a sample from 63 skulls of 38 species of the 6 genera. State I occurs in 38 species and the 6 genera, II in 4 species.

The range of variation in the relative length of the anterior portion of the skull is from 44.6 per cent (*Crotalus lepidus*) to 57.0 per cent (*C. atrox*). The maximum span in a single species is 5.0 per cent (*Trimeresurus stejnegeri*). However, 94.6 per cent of the species have a span of 4.0 per cent or less.

*Azemiops* has State II as sampled from two skulls: range is 41.4 per cent to 45.9 per cent; span of 4.6 per cent.

*Atractaspis* has State I in a sample from 7 skulls of 4 species. The range of variation in the relative length of the skull is from 46.7 per cent (*A. irregularis*) to 54.7 per cent (*A. microlepidota*).

## PHYLETICS OF CHARACTER 25

Character States II and III are rare in Colubridae (table 68) (Criterion 2).

State II, a relatively short anterior portion of the skull, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
  *Abastor erythrogrammus*
  *Achalinus spinalis*
  *Calamaria pavimentata*
    *septentrionalis*
  *Calamelaps unicolor*
  *Chilorhinophis carpenteri*
  *Diadophis regalis*
  *Dimades plicatilis*
  *Enhydris bocourti*
    *plumbea*
  *Helicops angulatus*
  *Limnophis bicolor*
  *Lycodon striatus*
  *Miodon gabonensis*
  *Natrix anoscopus*
    *ridiga*
  *Opisthotropis latouchi*
  *Rhynchocalamus melanocephalus*
  *Stilostoma extenuatum*
  *Storeria dekayi*
    *occipitomaculata*
Elapidae
  *Cacophis harriettae*
  *Calliophis japonicus*
  *Denisonia coronoides*
  *Elaps lacteus*
  *Hoplocephalus bitorquatus*
  *Leptomicrurus narducci*
  *Micrurus spixi*
  *Rhynchoelaps bertholdi*
  *Vermicella annulata*
Hydrophiidae
  *Hydrelaps darwiniensis*
  *Hydrophis cyanocinctus*
    *major*
    *ornatus*
  *Laticauda colubrina*
  *Microcephalophis cantoris*

Viperinae
*Adenorhinos barbouri*
*Atheris hindii*
*superciliaris*
*Bitis peringueyi*
*Cerastes vipera*
*Echis carinatus*
*Vipera ammodytes*
*aspis*
*berus*
*latasti*
Crotalinae
*Agkistrodon hypnale*
*nepa*
*piscivorus*
*Crotalus lepidus*
*Azemiops*

In these colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total working sample (table 69) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the aquatic (38.1 per cent) and secretive habitats (57.1 per cent) compared to the relative abundance of aquatic and secretive colubrid species in the total working sample (14.9 per cent; 23.2 per cent—table 70) (Criterion 5).

TABLE 69. Correlation of States II and III of Character 25 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | | | |
|---|---|---|---|---|---|---|
| | In species having State II of Character 25 | | In species having State III of Character 25 | | In total working sample | |
| 1 | 42.9% | (7)* | | | 14.3% | (28) |
| 2 | | | 81.8% | (8) | 15.6 | (31) |
| 7 | 61.9 | (11) | | | 25.5 | (56) |
| 9 | 23.8 | (4) | | | 6.8 | (14) |
| 11 | | | 45.5 | (4) | 26.7 | (50) |
| 13 | | | 45.5 | (4) | 31.8 | (54) |
| 19 | 80.0 | (13) | | | 36.8 | (68) |
| 22 | 23.8 | (4) | 27.3 | (2) | 4.5 | (11) |
| 28 | 22.2 | (4) | | | 11.7 | (26) |
| 29 | 30.0 | (6) | | | 10.1 | (27) |
| 31 | 40.0 | (7) | 36.4 | (4) | 19.5 | (44) |
| 32 | 43.8 | (7) | 45.5 | (5) | 26.3 | (55) |
| 33 | | | 63.6 | (6) | 43.0 | (76) |
| 34 | 21.1 | (4) | | | 6.8 | (18) |
| 35 | 15.0 | (3) | | | 2.0 | (6) |
| 36 | 19.0 | (4) | | | 6.1 | (16) |
| 38 | 30.0 | (6) | | | 16.2 | (27) |
| 39 | 23.8 | (4) | | | 9.0 | (15) |
| 41 | 27.8 | (5) | | | 10.9 | (20) |
| 42 | 50.0 | (9) | | | 8.7 | (14) |
| 44 | 14.3 | (3) | | | 5.8 | (11) |
| 46 | | | 63.6 | (6) | 26.9 | (52) |
| 48 | | | 30.0 | (3) | 6.2 | (11) |

* Number of genera.

The application of three criteria (2, 3, 5) suggests that State II is derived (Criterion 8).

State III, a relatively long anterior portion of the skull, occurs in the following colubrids in our working sample:

Colubridae
- *Lystrophis d'orbignyi*
- *Malpolon moilensis*
- *Oxybelis aeneus*
  - *fulgidus*
- *Passerita prasinus*
- *Psammophis subtaeniatus*
- *Pseudaspis cana*
- *Rhamphiophis oxyrhynchus*
- *Rhinostoma guianense*
- *Scaphiophis albopunctatus*
- *Xenodon severus*

In these colubrids this character state has a higher frequency of correlation with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total working sample (table 69) (Criterion 3).

Nine of these 11 colubrids have an anteriorly projecting premaxilla which is reflected in the projecting tip of the snout. In the terrestrial forms the snout is used for scooping soil in search of prey. The elongation of the snout in the arboreal taxa appears correlated with binocular fixation of prey. Sighting grooves and linear coloration of the snout are parts of this specialization (see Walls, 1942; Ficken et al., 1971). The morphological specialization criterion seems applicable (Criterion 4).

Also these colubrids have a markedly larger number of species confined to the terrestrial and arboreal habitats (54.5 per cent, 27.3 per cent) compared to the relative abundance of terrestrial and arboreal colubrid species in the total working sample (36.2 per cent, 16.5 per cent—table 70) (Criterion 5).

The application of four criteria (2, 3, 4, 5) suggests that State III is derived (Criterion 8).

TABLE 70. Habitat distribution of colubrid species having States II and III of Character 25 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 25 % | State III Character 25 % |
|---|---|---|---|
| Terrestrial | 36.2 | 4.8 | 54.5 |
| Arboreal | 16.5 | | 27.3 |
| Aquatic | 14.9 | 38.1 | |
| Subterrestrial | 10.8 | 23.8 | |
| Fossorial | 12.4 | 33.3 | 18.2 |
| Variation | 5.3 | | |
| Unknown | 3.5 | | |

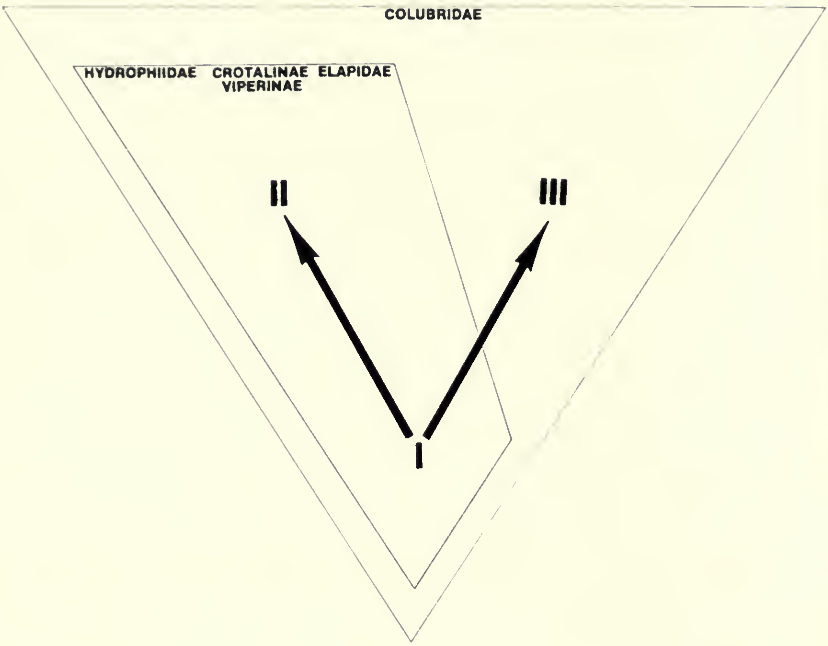

FIG. 24. Distribution among families of states of Characters 25 and 42. Direction of change among states shown by arrows.

State II probably arose in a different sequential direction than State III because State II correlates mostly with derived states of different characters (table 69) and is predominantly abundant in different habitat zones (table 70).

The nature of Character 25, linearly ordered by size (table 66, column 2) makes the sequential arrangement given of the three designated states the most probable.

Our interpretation of the phyletics of Character 25 is shown in Figure 24.

## Character 26—Relative Width of Skull

### DESCRIPTION OF CHARACTER

The relative width of the skull is here defined as the proportion of the total length of the skull formed by the width of the skull. The latter was measured at the fronto-parietal suture because this suture is a veritable midline in most taxa and affords an excellent

TABLE 71. Spans in relative width of skull by species and genera.

| | | Number of species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 232 | 150 | 22 | 17 | 17 | 26 |
| 2 | 3 | 3 | | | | |
| 3 | 2 | 1 | | | | 1 |
| 4 | 1 | | | | 1 | |
| 5 | 4 | 4 | | | | |
| 6 | 4 | 3 | 1 | | | |
| 7 | 5 | 4 | | | 1 | |
| 8 | 2 | 2 | | | | |
| 10 | 3 | 3 | | | | |
| 11 | 2 | 2 | | | | |
| 12 | 4 | 3 | 1 | | | |
| 13 | 1 | 1 | | | | |
| 14 | 3 | 1 | | 1 | | 1 |
| 15 | 3 | 1 | 1 | | 1 | |
| 16 | 1 | | | | | 1 |
| 17 | 3 | 3 | | | | |
| 18 | 4 | 3 | 1 | | | |
| 19 | 1 | 1 | | | | |
| 20 | 1 | | | 1 | | |
| 21–30 | 28 | 17 | 2 | 3 | 4 | 2 |
| 31–40 | 15 | 12 | | 1 | 2 | |
| 41–50 | 12 | 5 | 2 | 2 | 2 | 1 |
| 51–60 | 6 | 3 | | 2 | | 1 |
| 61–70 | 7 | 3 | | | 2 | 2 |
| 71–80 | 3 | | 2 | | | 1 |
| 81–90 | 2 | | | 1 | 1 | |
| 91–100 | 4 | 1 | | 1 | 1 | 1 |
| 105 | 1 | 1 | | | | |
| 116 | 1 | | | | | 1 |
| 118 | 1 | | | | 1 | |
| 214 | 1 | | | | 1 | |
| Total | 360 | 227 | 32 | 29 | 34 | 38 |
| Span 4.0% or less | 89.4% | 94.3% | 87.5% | 79.3% | 76.5% | 81.6% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

constant reference point for measurements (see Character 25, table 66).

### CLASSES AND STATES

The total range of variation in relative width of the skull was segmented by steps of 4.0 per cent, since a span of 4.0 per cent covered most of the intraspecific variation encountered (89.4 per cent—table 71). Ten classes resulted as shown in Table 72. The mean of each taxon was assigned to a class (table 72). States are established when there is a marked change in frequency of number of species between classes.

TABLE 72. Frequency distribution of species in range classes of relative width of the skull in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 13.3–17.2 | 7/1 | 4/2 | | | |
| 2 | 17.3–21.2 | 36/19 | 6/5 | 9/4 | 1/0 | |
| 3 | 21.3–25.2 | 65/34 | 6/5 | 6/2 | | |
| 4 | 25.3–29.2 | 51/29 | 11/8 | 9/3 | 6/1 | 2/0 |
| 5 | 29.3–33.2 | 38/25 | 4/4 | 3/1 | 9/3 | 5/0 |
| 6 | 33.3–37.2 | 22/9 | 1/1 | 2/1 | 11/2 | 6/2 |
| 7 | 37.3–41.2 | 6/2 | | | 2/1 | 14/2 |
| 8 | 41.3–45.2 | 2/0 | | | 2/1 | 4/1 |
| 9 | 45.3–49.2 | | | | 2/0 | 6/1 |
| 10 | 49.3–53.2 | | | | 1/0 | 1/0 |
| Totals | | 227/119 | 32/25 | 29/11 | 34/8 | 38/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 73. Distribution of character states of relative width of the skull.

| | STATES | | | |
|---|---|---|---|---|
| | IV | I | II | III |
| Classes[1] | 1 | 2–6 | 7–8 | 9–10 |
| | | SPECIES | | |
| Colubridae —227 | 3.1% | 93.4% | 3.5% | |
| Elapidae — 32 | 12.5 | 87.5 | | |
| Hydrophiidae— 29 | | 100.0 | | |
| Viperinae — 34 | | 79.4 | 11.8 | 8.8% |
| Crotalinae — 38 | | 34.2 | 47.4 | 18.4 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 4 | | 100.0 | | |
| | | GENERA | | |
| Colubridae —119 | 0.8% | 97.5 | 1.7 | |
| Elapidae — 25 | 8.0 | 92.0 | | |
| Hydrophiidae— 11 | | 100.0 | | |
| Viperinae — 8 | | 75.0 | 25.0 | |
| Crotalinae — 6 | | 33.3 | 50.0 | 16.7 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 1 | | 100.0 | | |

[1] See Table 72.

Four states are recognized:

State I —Classes 2–6 (17.3–37.2 per cent)
State II —Classes 7–8 (37.3–45.2)
State III—Classes 9–10 (45.3–53.2)
State IV—Class 1 (13.3–17.2)

### Familial Ranges of Variation (Table 73)

Colubridae—This family has States I, II, and IV in a sample from 379 skulls of 227 species of 119 genera. State I occurs in 212 species and 116 genera, II in 8 species and 2 genera, IV in 7 species and 1 genus.

The range of variation in the relative width of the skull is from 13.3 per cent (*Passerita nasuta*) to 43.9 per cent (*Mehelya chanleri*). The maximum span in a single species is 10.5 per cent (*Opheodrys vernalis*). However, 94.3 per cent of the species have a span of 4.0 per cent or less.

Elapidae—This family has States I and IV in a sample from 51 skulls of 32 species of 25 genera. State I occurs in 28 species and 23 genera, IV in 4 species and 2 genera.

The range of variation in the relative width of the skull is from 14.4 per cent (*Micrurus fulvius*) to 37.2 per cent (*Ophiophagus hannah*). The maximum span in a single species is 7.7 per cent (*Vermicella annulata*). However, 87.5 per cent of the species have a span of 4.0 per cent or less.

Hydrophiidae—The sea snakes only have State I in a sample from 67 skulls of 29 species of 11 genera.

The range of variation in the relative width of the skull is from 16.3 per cent (*Hydrophis cyanocinctus*) to 37.8 per cent (*Laticauda semifasciata*). The maximum span in a single species is 9.9 per cent (*L. semifasciata*). However, 79.3 per cent of the species have a span of 4.0 per cent or less.

Viperinae—The true vipers have States I, II, and III in a sample from 90 skulls of 34 species of the 8 genera. State I occurs in 27 species and 6 genera, II in 4 species and 2 genera, III in 3 species.

The range of variation in the relative width of the skull is from 20.3 per cent (*Vipera aspis*) to 60.6 per cent (*Bitis gabonica*). The maximum span in a single species is 21.4 per cent (*B. gabonica*). However, 76.5 per cent of the species have a span of 4.0 per cent or less.

Crotalinae—The pit vipers have States I, II, and III in a sample from 63 skulls of 38 species of the 6 genera. State I occurs in 13 species and 2 genera, II in 18 species and 3 genera, III in 7 species and 1 genus.

The range of variation in the relative width of the skull is from 25.5 per cent (*Crotalus lepidus*) to 57.0 per cent (*Trimeresurus wagleri*). The maximum span in a single species is 11.6 per cent (*Trimeresurus wagleri*). However, 81.6 per cent of the species have a span of 4.0 per cent or less.

*Azemiops* has State I in a sample from three skulls; range is 31.0–31.8 per cent; span of 0.9 per cent.

*Atractaspis* has State I in a sample from six skulls of four species. The range of variation in the relative width of the skull is from 24.8 per cent (*A. irregularis*) to 32.8 per cent (*A. microlepidota*). The maximum span is 3.7 per cent (*A. microlepidota*).

### PHYLETICS OF CHARACTER 26

Character States II and IV are very rare in Colubridae (table 73) (Criterion 2).

State II, a relatively wide skull, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Boiga blandingi*
    - *dendrophila*
    - *jaspidea*
  - *Chilomeniscus cinctus*
  - *Holarchus hainonensis*
  - *Lystrophis semicinctus*
  - *Mehelya chanleri*
  - *Rhynchocalamus melanocephalus*
- Viperinae
  - *Atheris chlorechis*
    - *hispidus*
    - *nitschei*
    - *squamiger*
- Crotalinae
  - *Agkistrodon acutus*
    - *bilineatus*
    - *contortrix*
    - *piscivorus*
    - *rhodostoma*
  - *Bothrops alternatus*
    - *cotiara*
    - *jararacussu*
    - *schlegeli*
  - *Crotalus durissus*
    - *pusillus*
    - *viridis*
  - *Trimeresurus albolabris*
    - *jerdoni*
    - *monticola*
    - *puniceus*
    - *stejnegeri*
    - *sumatranus*

In these colubrids this character state has a higher frequency of correlation with derived states of 12 other characters compared to the frequency distribution of these states of the same 12 characters in the total working sample (table 74) (Criterion 3).

TABLE 74. Correlation of States II and IV of Character 26 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 26 | In species having State IV of Character 26 | In total working sample |
| 2 | | 71.4% (3)* | 15.6% (31) |
| 4 | 37.5% (1) | | 3.8 (4) |
| 11 | | 42.9 (3) | 26.7 (50) |
| 13 | 50.0 (2) | 71.4 (3) | 31.8 (54) |
| 16 | 37.5 (2) | | 21.7 (34) |
| 20 | 62.5 (3) | | 41.2 (74) |
| 21 | 75.0 (4) | | 18.9 (29) |
| 22 | 37.5 (2) | 71.4 (3) | 4.5 (11) |
| 25 | | 42.9 (3) | 6.3 (12) |
| 31 | 42.9 (2) | | 19.5 (44) |
| 32 | | 50.0 (2) | 26.3 (55) |
| 33 | 75.0 (4) | | 43.0 (76) |
| 40 | 50.0 (3) | | 24.8 (54) |
| 41 | 37.5 (2) | | 10.9 (20) |
| 42 | 37.5 (2) | | 8.7 (14) |
| 46 | 50.0 (2) | 83.3 (3) | 26.9 (52) |

* Number of genera.

TABLE 75. Habitat distribution of colubrid species having States II and IV of Character 26 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 26 % | State IV Character 26 % |
|---|---|---|---|
| Terrestrial | 36.2 | 37.5 | 14.3 |
| Arboreal | 16.5 | 37.5 | 71.4 |
| Aquatic | 14.9 | | |
| Subterrestrial | 10.8 | | 14.3 |
| Fossorial | 12.4 | 25.0 | |
| Variation | 5.3 | | |
| Unknown | 3.5 | | |

The application of two criteria (2, 3) suggests that State II is derived (Criterion 8).

Character State III, a very wide skull, does not occur in the colubrids and is present only in the vipers. We apply the uniqueness criterion (1) to Character State III, for its presence is unique to a derived stock.

The taxa having State III are:

Viperinae
- *Bitis arietans*
  - *gabonica*
  - *nasicornis*

Crotalinae
- *Crotalus adamanteus*
  - *atrox*
  - *horridus*
  - *molossus*
  - *ruber*
- *Lachesis mutus*
- *Trimeresurus wagleri*

State IV, a relatively narrow skull, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Enhydris bocourti*
- *Malpolon monspessulanus*
- *Oxybelis aeneus*
  - *argenteus*
- *Passerita nasuta*
  - *prasinus*
- *Uromacer oxyrhynchus*

Elapidae
- *Micruroides euryxanthus*
- *Micrurus fulvius*
  - sp.
  - *spixi*

In these colubrids this character state has a higher frequency of correlation with derived states of seven other characters compared to the frequency distribution of these states of the same seven characters in the total working sample (table 74) (Criterion 3).

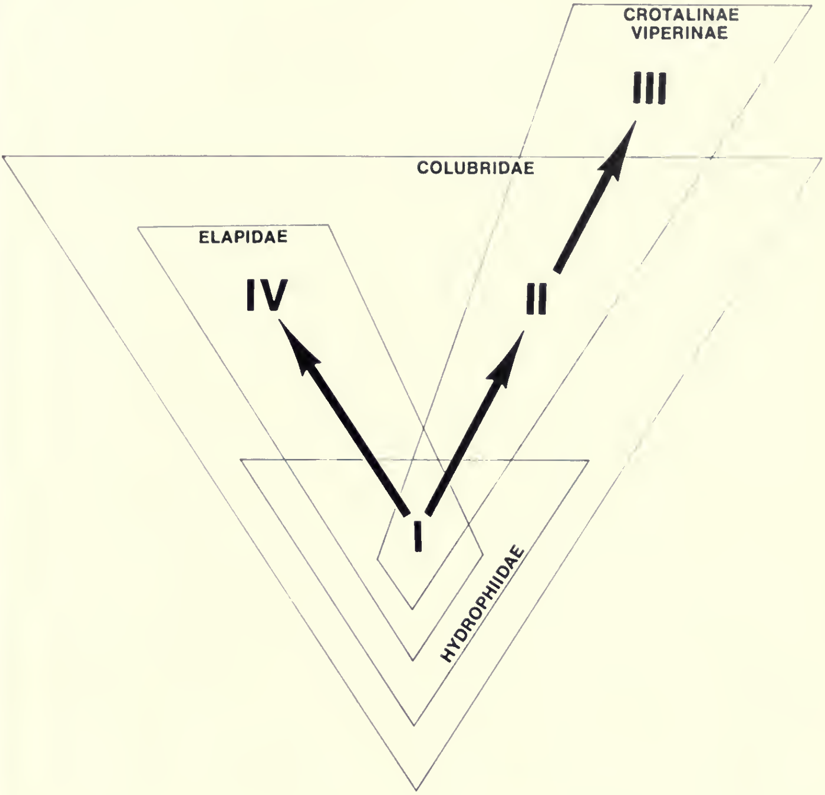

FIG. 25. Distribution among families of states of Character 26. Direction of change among states shown by arrows.

Also these colubrids have a markedly larger number of species confined to the arboreal habitat (71.4 per cent) compared to the relative abundance of arboreal colubrid species in the total working sample (16.5 per cent—table 75) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State IV is derived (Criterion 8).

State IV (a narrow skull) probably arose in a different sequential direction than State II because State IV correlates mostly with derived states of different characters (table 74).

The nature of Character 26, linearly ordered by size (table 72—Column 2), makes the arrangement given of the four designated states most probable.

Our interpretation of the phyletics of Character 26 is shown in Figure 25.

## Character 27—Posterior Process From Lateral Arms of Premaxilla

### DESCRIPTION OF CHARACTER

The premaxillary bone has lateral arms. Each lateral arm may have a posteriorly directed process.

Three states are recognized:

State I —process absent
State II —process present
State III—intraspecific variation, both States I and II present

### FAMILIAL RANGES OF VARIATION (Table 76)

Colubridae—This family has all three states in a sample of 280 species of 157 genera (535 skulls). State I occurs in 230 species of 125 genera (437 skulls), II in 49 species of 39 genera (95 skulls), III occurs in monotypic *Farancia* (3 skulls).

Intrageneric variation occurs in 10 genera (*Clelia, Farancia, Leptodeira, Psammophis, Ptyas, Pseudoboa, Sonora, Stegonotus, Tachymenis, Xenodon*).

Elapidae—This family has States I and II in a sample of 60 species of 36 genera (98 skulls). State I occurs in 10 species of 10 genera (12 skulls), II in 50 species of 27 genera (86 skulls).

Intrageneric variation occurs in *Leptomicrurus*.

Hydrophiidae—The sea snakes only have State I in a sample of 38 species of 13 genera (130 skulls).

Viperinae—The true vipers have States I and II in a sample of 32 species of the 8 genera (93 skulls). State I occurs in 31 species of 7 genera (91 skulls), II occurs in the monotypic *Adenorhinos* (2 skulls).

Crotalinae—The pit vipers have State I in a sample of 44 species of the 6 genera (83 skulls).

*Azemiops* has State I (2 skulls).

*Atractaspis* has State I in a sample of 4 species (7 skulls).

TABLE 76. Distribution of character states of the posterior process from the lateral arm of the premaxilla.

| | | STATES | | |
|---|---|---|---|---|
| | I | II | III | |
| Description | Absent | Present | Intraspecific Variation | |
| | | SPECIES | | |
| Colubridae —280 | 82.1% | 17.5% | 0.4% | |
| Elapidae — 60 | 16.7 | 83.3 | | |
| Hydrophiidae— 38 | 100.0 | | | |
| Viperinae — 32 | 96.9 | 3.1 | | |
| Crotalinae — 44 | 100.0 | | | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 4 | 100.0 | | | |
| | | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —157 | 74.5 | 19.7 | | 5.7% |
| Elapidae — 36 | 25.0 | 72.2 | | 2.8 |
| Hydrophiidae— 13 | 100.0 | | | |
| Viperinae — 8 | 87.5 | 12.5 | | |
| Crotalinae — 6 | 100.0 | | | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

## Phyletics of Character 27

Character State II is not particularly rare in the colubrids (table 76). It occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Abastor erythrogrammus*
  - *Clelia fitzingeri*
  - *Conopsis lineatus*
    - *nasus*
  - *Coronella austriaca*
  - *Cyclagras gigas*
  - *Dinodon rufozonatum*
  - *Drymarchon corais*
  - *Dugandia bicolor*
  - *Gastropyxis smaragdina*
  - *Gonyosoma oxycephalum*
  - *Holuropholis olivaceus*
  - *Hydrodynastes gigas*
  - *Lampropeltis elapsoides*
    - *getulus*
    - *triangulus*
  - *Leptodeira annulata*
  - *Leptophis mexicanus*
    - *occidentalis*
  - *Lioheterodon madagascariensis*
  - *Liopholidophis lateralis*
  - *Lycodon aulicus*
    - *striatus*
  - *Miodon gabonensis*
  - *Oxyrhopus petola*
  - *Prosymna ambiguia*
  - *Psammodynastes pictus*
    - *pulverulentus*
  - *Psammophis sibilans*
  - *Psammophylax rhombeatus*
  - *Pseudoboa claelia*
    - *clathrata*
    - *haasi*
  - *Pseudorhabdion longiceps*
  - *Pseudoxenodon sinensis*
  - *Pseustes poecilonotus*
    - *sulphureus*
  - *Ptyas korros*
  - *Rhacidelus brazili*
  - *Rhamphiophis oxyrhynchus*
  - *Simophis rhinostoma*
  - *Siphlophis cervinus*
  - *Sonora episcopa*
  - *Spilotes pullulatus*
  - *Stegonotus magnus*
  - *Tachymenis peruviana*
  - *Tantilla gracilis*
  - *Telescopus iberus*
  - *Xenodon merremii*
- Elapidae
  - *Apistocalamus lonnbergi*
    - *loriae*
  - *Aspidomorphus lineaticollis*
    - *muelleri*
  - *Boulengerina annulata*
  - *Brachyaspis curta*
  - *Bungarus candidus*
    - *fasciatus*
    - *multicinctus*
  - *Cacophis harriettae*
  - *Calliophis japonicus*
  - *Demansia olivacea*
    - *textilis*
  - *Dendroaspis angusticeps*
    - *jamesoni*
    - *viridis*
  - *Denisonia coronoides*
    - *fasciatus*
    - *nigrescens*
    - *superba*
    - *woodfordi*
  - *Elapsoidea sundevalli*
  - *Hoplocephalus bungaroides*
  - *Leptomicrurus collaris*
  - *Maticora bivirgata*
  - *Micropechis elapsoides*
    - *ikaheka*
  - *Micrurus affinis*
    - *fulvius*
    - *lemniscatus*
    - *mipartitus*
    - *nigrocinctus*
    - *spixi*
  - *Naja haje*
    - *melanoleuca*
    - *naja*
    - *nigricollis*
    - *nivea*

*Notechis scutatus*
*Ogmodon vitianus*
*Ophiophagus hannah*
*Oxyuranus scutellatus*
*Parapistocalamus hedigeri*
*Pseudechis australis*
  *papuanus*
  *porphyriacus*
*Pseudohaje goldii*
*Toxicocalamus stanleyanus*
*Vermicella annulata*
*Walterinnesia aegyptia*

In these colubrids, character State II has higher frequencies of correlation with derived states of four other characters compared to the frequency distributions of these states of the same four characters in the total working sample (table 77) (Criterion 3).

TABLE 77. Correlation of State II of Character 27 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State II of Character 27 | In total working sample |
| 5 | 8.3% (3)* | 3.5% (9) |
| 37 | 34.7 (15) | 22.9 (54) |
| 40 | 37.5 (16) | 24.8 (54) |
| 46 | 37.5 (15) | 27.8 (52) |

* Number of genera.

Also these colubrids have a larger number of species confined to the terrestrial habitat (49.0 per cent) compared to the abundance of terrestrial colubrid species in the working total sample (36.2 per cent—table 78) (Criterion 5).

Although not statistically significant, the data suggest that two criteria (3, 5) are applicable and that State II is derived.

TABLE 78. Habitat distribution of colubrid species having State II of Character 27 compared to frequencies in the total colubrid working sample.

| | Total Working Sample % | State II Character 27 % |
|---|---|---|
| Terrestrial | 36.2 | 49.0 |
| Arboreal | 16.5 | 12.2 |
| Aquatic | 14.9 | 8.2 |
| Subterrestrial | 10.8 | 8.2 |
| Fossorial | 12.4 | 8.2 |
| Variation | 5.3 | 8.2 |
| Unknown | 3.5 | 6.1 |

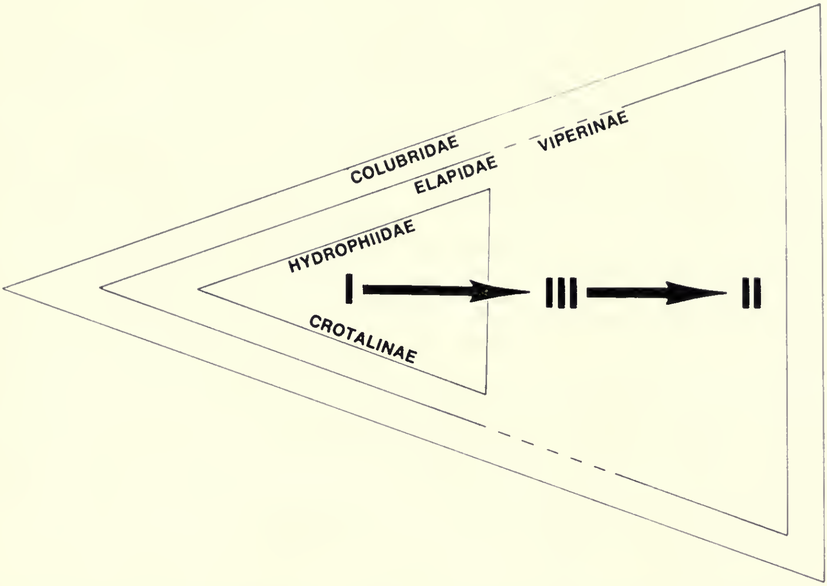

Fig. 26. Distribution among families of states of Character 27. Direction of change among states shown by arrows.

State III occurs in the colubrid *Farancia abacura*. State III is by definition an intermediate state because each taxon with this state has both states I and II.

Our interpretation of the phyletics of this character 27 is shown in Figure 26.

## Character 28—Vomer Ring

### Description of Character

In snakes the bones forming part of the roof of the mouth just posterior to the premaxilla have been called the vomers and prevomers. Peters (1964, p. 383) discusses the nomenclature of these bones. We use the name vomer without making any judgment as to the bone's ultimate homology.

The vomers have an inferior posterior process or lamina. The lamina is often widely fenestrated, forming a bony ring. This ring, when present, is in the vertical plane, and is not to be confused with the antero-ventral vomeronasal fenestra which is situated in the horizontal plane and readily visible from the ventral view. Von Szunyoghy (1932) pointed out the taxonomic value of variations in the vomer. There may be considerable intrageneric variation in the shape of the fenestra (e.g., Duellman, 1958, fig. 17), but we are here only concerned with gross characterization as follows:

State I —lamina fenestrated, ring complete
State II —lamina deeply emarginated (ring incomplete) or part of lamina absent
State III—intraspecific variation (I and II)
State IV—lamina completely ossified, lacking hole

### FAMILIAL RANGES OF VARIATION (Table 79)

Colubridae—This family has all four states in a sample of 273 species of 147 genera (524 skulls). State I occurs in 241 species of 126 genera (470 skulls), II in 27 species of 21 genera (42 skulls), III in 3 species of 3 genera (9 skulls), IV in 2 species of 2 genera (3 skulls).

Intrageneric variation occurs in three genera having States I and II (*Atractus, Enhydris, Pseudoboa*).

Elapidae—This family has States I, II, and III in a sample of 49 species of 32 genera (90 skulls). State I occurs in 37 species of 25 genera (72 skulls), II in 11 species of 10 genera (15 skulls), III in 1 species (3 skulls).

Intrageneric variation occurs in *Bungarus* which has States I and III.

Hydrophiidae—The sea snakes have States I, II, and III in a sample of 36 species of the 16 genera (134 skulls). State I occurs in 6 species of 5 genera (30 skulls), II in 28 species of 14 genera (86 skulls), III in 2 species of *Hydrophis* (18 skulls).

Intrageneric variation occurs in three genera: *Hydrophis* (I, II, III), *Aipysurus, Laticauda* (I, II).

Viperinae—The true vipers have States I, II, and III in a sample of 30 species of the 8 genera (98 skulls). State I occurs in 22 species of 7 genera (71 skulls), II in 7 species of 2 genera (24 skulls), III in 1 species (3 skulls).

Intrageneric variation occurs in 2 genera, *Atheris* (I, II) and *Echis* (I, III).

Crotalinae—The pit vipers have States I, II, and IV in a sample of 42 species of the 6 genera (79 skulls). State I occurs in 29 species of 6 genera (59 skulls), II in 9 species of 4 genera (12 skulls), IV in 4 species of 3 genera (8 skulls).

## TABLE 79. Distribution of character states of the vomer ring.

| | STATES | | | | INTRAGENERIC VARIATION | | | |
|---|---|---|---|---|---|---|---|---|
| | IV | I | III | II | I, II, III | I, III | I, II | I, II, IV |
| Description | Solid | Ringed | Intraspecific Variation: I and II | Not Ringed | | | | |
| | | | SPECIES[1] | | | | | |
| Colubridae —273 | 0.7% | 88.3% | 1.1% | 9.9% | | | | |
| Elapidae — 49 | | 75.5 | 2.0 | 22.4 | | | | |
| Hydrophiidae— 36 | | 16.7 | 5.6 | 77.8 | | | | |
| Viperinae — 30 | | 73.3 | 3.3 | 23.3 | | | | |
| Crotalinae — 42 | 9.5 | 69.0 | | 21.4 | | | | |
| *Azemiops* — 1 | | 100.0 | | | | | | |
| *Atractaspis* — 5 | | | | 100.0 | | | | |
| | | | GENERA | | | | | |
| Colubridae —147 | 1.4 | 82.3 | 2.0 | 12.2 | | | 2.0% | |
| Elapidae — 32 | | 65.6 | | 31.3 | 3.1% | | | |
| Hydrophiidae— 16 | | 12.5 | | 68.8 | 6.3 | | 12.5 | |
| Viperinae — 8 | | 62.5 | | 12.5 | | 12.5% | 12.5 | |
| Crotalinae — 6 | | 33.3 | | | | | 16.7 | 50.0% |
| *Azemiops* — 1 | | 100.0 | | | | | | |
| *Atractaspis* — 1 | | | | 100.0 | | | | |

[1] Working sample.

Intrageneric variation occurs in 4 genera: *Agkistrodon, Bothrops, Trimeresurus* (I, II, IV), and *Crotalus* (I, II).

*Azemiops* has State I (2 skulls).

*Atractaspis* has State II in a sample of 5 species (8 skulls).

### PHYLETICS OF CHARACTER 28

Character State II is rare in the colubrids (table 79) (Criterion 2).

State II, vomer ring incomplete or absent, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Achalinus spinalis*
  - *Aparallactus lunulatus*
    - *werneri*
  - *Atractus elaps*
    - *erythromelas*
  - *Calamaria leucogaster*
    - *linnaei*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Crotaphopeltis hotamboeia*
  - *Dipsadoboa unicolor*
  - *Dryadophis amarali*
  - *Enhydris plumbea*
  - *Geophis semidoliatus*
  - *Haldea striatula*
  - *Oxyrhabdium modestum*
  - *Oxyrhopus petola*
  - *Psammodynastes pictus*
    - *pulverulentus*
  - *Pseudorhabdion longiceps*
  - *Prosymna ambigua*
  - *Pseudoboa neuwiedii*
  - *Rhacidelus brazili*
  - *Sibon sibon*
  - *Tropidocloniom lineatum*
  - *Tropidodipsas fischeri*
- Elapidae
  - *Apistocalamus loriae*
  - *Aspidomorphus lineaticollis*
  - *Brachyaspis curta*
  - *Dendroaspis angusticeps*
    - *viridis*
  - *Elaps lacteus*
  - *Elapsoidea sundevalli*
  - *Furina diadema*
  - *Leptomicrurus narducci*
  - *Ogmodon vitianus*
  - *Rhynchoelaps bertholdi*
- Hydrophiidae
  - *Acalyptophis peronii*
  - *Aipysurus eydouxi*
    - *foliosquama*
    - *fuscus*
  - *Astrotia stokesii*
  - *Emydocephalus ijimae*
  - *Enhydrina schistosa*
  - *Ephalophis greyi*
  - *Hydrelaps darwiniensis*
  - *Hydrophis belcheri*
    - *brookii*
    - *caerulescens*
    - *inornatus*
    - *klossi*
    - *lapemoides*
    - *melanocephalus*
    - *melanosoma*
    - *mertoni*
    - *ornatus*
    - *torquatus*
  - *Kerilia jerdoni*
  - *Lapemis curtus*
    - *hardwickii*
  - *Laticauda semifasciata*
  - *Microcephalophis cantoris*
    - *gracilis*
  - *Thalassophina viperina*
  - *Thalassophis anomalus*
- Viperinae
  - *Atheris hispidus*
    - *squamiger*
  - *Causus*

Crotalinae
*Agkistrodon contortrix*
*halys*
*nepa*
*rhodostoma*
*Bothrops dunni*
*Crotalus basiliscus*
*ruber*
*Trimeresurus albolabris*
*sumatranus*

In these colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total sample (table 80) (Criterion 3).

TABLE 80. Correlation of State II of Character 28 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State II of Character 28 | In total working sample |
| 1 | 25.9% (4)* | 14.3% (28) |
| 7 | 59.3 (11) | 25.5 (26) |
| 9 | 22.2 (3) | 6.8 (14) |
| 13 | 44.4 (9) | 31.8 (54) |
| 19 | 70.4 (12) | 36.8 (68) |
| 24 | 18.5 (4) | 3.8 (11) |
| 27 | 30.0 (5) | 17.9 (40) |
| 29 | 23.1 (5) | 10.1 (27) |
| 31 | 34.8 (7) | 19.5 (44) |
| 34 | 27.3 (5) | 6.8 (18) |
| 36 | 23.1 (6) | 6.1 (16) |
| 38 | 40.0 (5) | 16.2 (27) |
| 39 | 25.0 (3) | 9.0 (15) |
| 40 | 42.3 (9) | 24.8 (54) |
| 42 | 33.3 (4) | 8.7 (14) |
| 49 | 40.0 (7) | 15.5 (26) |
| 50 | 52.6 (6) | 20.0 ( 6 ) |

* Number of genera.

These colubrids also have a markedly larger number of species confined to the fossorial habitat (48.1 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (table 81) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

State III is also rare in the colubrids (Criterion 2).

State III, intraspecific variation of States I and II, occurs in the following colubrids (plus other taxa):

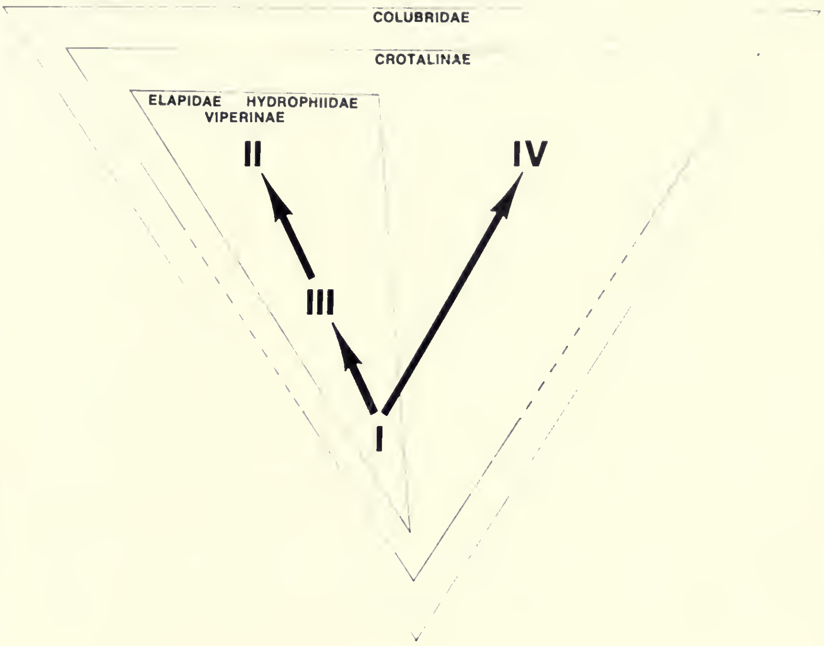

FIG. 27. Distribution among families of states of Character 28. Direction of change among states shown by arrows.

Colubridae
*Darlingtonia haetiana*
*Drymarchon corais*
*Spalerosophis diadema*
Elapidae
*Bungarus fasciatus*
Hydrophiidae
*Hydrophis cyanocinctus*
*fasciatus*

Viperinae
*Echis coloratus*

State III is an intermediate sequential state between I and II because each taxon with this state has both States I and II.

State IV is also very rare in the colubrids (Criterion 2).

State IV, the complete ossification of the lamina, only occurs in four crotalinaes and in two different adaptive types of fossorial colubrid species of our sample, the South American *Apostolepis ambinigra* and the African *Scaphiophis albopunctatus*. These two species are so widely separated geographically and burrow so differently (blunt-headed and shovel-snouted) that this character state (IV) must have evolved separately in the Colubridae. Our interpretation is that this state almost certainly arose from a complete vomer ring (State I) rather than from the loss of the ring (State II) for it seems that

TABLE 81. Habitat distribution of colubrid species having State II of Character 28 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 28 % |
|---|---|---|
| Terrestrial | 36.2 | 11.1 |
| Arboreal | 16.5 | 11.1 |
| Aquatic | 14.9 | 3.7 |
| Subterrestrial | 10.8 | 14.8 |
| Fossorial | 12.4 | 48.1 |
| Variation | 5.3 | 7.4 |
| Unknown | 3.5 | 3.7 |

it would be much less complicated genetically and morphologically to fill a fenestra than to lose most of the process and then replace it with new osteological material.

Our interpretation of the phyletics of Character 28 is shown in Figure 27.

## Character 29—Lateral Process of Palatine

### DESCRIPTION OF CHARACTER

The palatine bone may have a process which extends laterally toward the maxilla, and is often referred to as a maxillary process (e.g., Albright and Nelson, 1959, p. 200). The process varies in its shape and positional relationship to the main shaft of the palatine bone. We have described the variation as encompassing four states:

State I —lateral process absent

State II —lateral process anteriorly directed

State III—lateral process posteriorly directed

State IV—lateral process laterally directed

### FAMILIAL RANGES OF VARIATION (Table 82)

Colubridae—This family has all four states in a sample of 298 species of 161 genera (548 skulls). State I occurs in 3 species of 3 genera (5 skulls), II in 13 species of 11 genera (17 skulls), III in 268 species of 140 genera (500 skulls), IV in 14 species of 14 genera (26 skulls).

Intrageneric variation occurs in seven genera: *Enhydris* and *Tropidodipsas* have States I and III; *Lycodon, Mehelya, Ninia,* and *Rhadinaea* have States III and IV; *Dasypeltis* has States II and IV.

TABLE 82. Distribution of character states of the lateral process of the palatine.

| | STATES | | | | INTRAGENERIC VARIATION | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | III | IV | II | I | III, IV | III, II | III, I | IV, II | IV, I |
| Description | Posterior | Lateral | Anterior | Absent | | | | | |
| | SPECIES[1] | | | | | | | | |
| Colubridae —298 | 89.9% | 4.7% | 4.4% | 1.0% | | | | | |
| Elapidae — 66 | 9.1 | 16.7 | 28.8 | 45.5 | | | | | |
| Hydrophiidae— 41 | 19.5 | 2.4 | 2.4 | 75.6 | | | | | |
| Viperinae — 33 | | | | 100.0 | | | | | |
| Crotalinae — 43 | | | | 100.0 | | | | | |
| *Azemiops* — 1 | | | | 100.0 | | | | | |
| *Atractaspis* — 5 | | | 100.0 | | | | | | |
| | GENERA | | | | | | | | |
| Colubridae —161 | 83.2 | 5.6 | 6.2 | 0.6 | 2.5% | | 1.2% | 0.6% | |
| Elapidae — 38 | 5.3 | 10.5 | 31.6 | 44.7 | | | 2.6 | | 5.3% |
| Hydrophiidae— 16 | 6.3 | 6.3 | | 75.0 | | 6.3% | 6.3 | | |
| Viperinae — 8 | | | | 100.0 | | | | | |
| Crotalinae — 6 | | | | 100.0 | | | | | |
| *Azemiops* — 1 | | | | 100.0 | | | | | |
| *Atractaspis* — 1 | | | 100.0 | | | | | | |

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[1] Working sample.

Elapidae—This family has all four states in a sample of 66 species of 38 genera (108 skulls). State I occurs in 30 species of 20 genera (44 skulls), II in 19 species of 12 genera (42 skulls), III in 6 species of 3 genera (8 skulls), IV in 11 species of 6 genera (14 skulls).

Intrageneric variation occurs in three genera: *Denisonia* has States I and III; *Apistocalamus* and *Aspidomorphus* have States I and IV.

Hydrophiidae—The sea snakes have all four states in a sample of 41 species of the 16 genera (142 skulls). State I occurs in 31 species of 13 genera (102 skulls), II in *Laticauda schistorhynchus* (1 skull), III in 8 species of 3 genera (38 skulls), IV in monotypic *Kolpophis* (1 skull).

Intrageneric variation occurs in two genera: *Laticauda* has States II and III; *Hydrophis* has States I and III.

Viperinae, Crotalinae, *Azemiops*—The true vipers, pit vipers, and *Azemiops* only have State I in a sample of 77 species (33, 43, 1, respectively) of the 15 genera (8, 6, 1) (176 skulls: 94, 80, 2).

*Atractaspis* only has State II in a sample of 5 species (8 skulls).

## PHYLETICS OF CHARACTER 29

Character State I is extremely rare in the colubrids (table 82) (Criterion 2). State I, absence of the lateral process of the palatine, occurs in the following colubrids (plus other taxa):

- Colubridae
    - *Enhydris bocourti*
    - *Sibon sibon*
    - *Tropidodipsas fischeri*
- Elapidae
    - *Acanthophis antarcticus*
    - *Apistocalamus lonnbergi*
    - *Aspidomorphus muelleri*
    - *Brachyaspis curta*
    - *Brachyurophis semifasciata*
    - *Cacophis harriettae*
    - *Demansia olivacea*
        - *textilis*
    - *Dendroaspis angusticeps*
        - *jamesoni*
        - *polylepis*
        - *viridis*
    - *Denisonia coronoides*
        - *fasciata*
        - *nigrescens*
        - *superba*
    - *Elapognathus minor*
    - *Furina diadema*
    - *Glyphodon tristis*
    - *Hoplocephalus bitorquatus*
        - *bungaroides*
    - *Notechis scutatus*
    - *Ogmodon vitianus*
    - *Oxyuranus scutellatus*
    - *Parapistocalamus hedigeri*
    - *Pseudechis australis*
        - *papuanus*
        - *porphyriacus*
    - *Rhynchoelaps bertholdi*
    - *Vermicella annulata*
- Hydrophiidae
    - *Acalyptophis*
    - *Aipysurus*

- *Astrotia*
- *Emydocephalus*
- *Enhydrina*
- *Ephalophis*
- *Hydrelaps*
- *Hydrophis belcheri*
  - *caerulescens*
  - *cyanocinctus*
  - *fasciatus*
  - *inornata*
  - *kingi*
  - *lapemoides*
  - *major*
  - *mamillaris*
  - *melanocephalus*
  - *melanosoma*
  - *mertoni*
  - *ornatus*
- *Kerilia*
- *Lapemis*
- *Pelamis*
- *Thalassophina*
- *Thalassophis*
- Viperinae (all taxa)
- Crotalinae (all taxa)
- *Azemiops*

Character State II is rare in the colubrids (table 82) (Criterion 2).

State II, an anteriorly directed lateral process, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Abastor erythrogrammus*
  - *Aparallactus lunulatus*
    - *werneri*
  - *Apostolepis ambinigra*
  - *Calamelaps unicolor*
  - *Conopsis nasus*
  - *Dasypeltis fasciatus*
    - *scabra*
  - *Dryocalamus davisoni*
  - *Duberria lutrix*
  - *Elapomorphus blumii*
  - *Miodon gabonensis*
  - *Sonora episcopa*
- Elapidae
  - *Aspidelaps*
  - *Boulengerina annulata*
  - *Calliophis japonicus*
  - *Elaps lacteus*
  - *Hemachatus haemachatus*
  - *Maticora bivirgata*
  - *Micropechis elapsoides*
  - *Micruroides euryxanthus*
  - *Naja*
  - *Ophiophagus hannah*
  - *Pseudohaje*
  - *Walterinnesia aegyptia*
- Hydrophiidae
  - *Laticauda schistorhynchus*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of 15 other characters compared to the frequency distribution of these states of the same 15 characters in the total sample (table 83) (Criterion 3).

These colubrids also have a significantly larger number of species confined to the secretive habitats (subterrestrial and fossorial—77.0 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (table 84) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

Character State IV is rare in the colubrids (table 82) (Criterion 2).

TABLE 83. Correlation of States II and IV of Character 29 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 29 | In species having State IV of Character 29 | In total working sample |
| 7 | 92.3% (11)* | 42.9% (6) | 25.5% (56) |
| 13 | 69.2 (7) | | 31.8 (54) |
| 19 | 53.8 (6) | | 36.8 (68) |
| 31 | 41.7 (5) | | 19.5 (44) |
| 32 | 88.9 (7) | 41.7 (5) | 26.3 (55) |
| 34 | 33.3 (3) | 23.1 (3) | 6.8 (18) |
| 35 | 27.3 (3) | 18.2 (2) | 2.0 ( 6 ) |
| 36 | 27.3 (3) | 23.1 (3) | 6.1 (16) |
| 38 | 37.5 (3) | 37.5 (3) | 16.2 (27) |
| 39 | 40.0 (3) | | 9.0 (15) |
| 40 | 53.8 (6) | 46.2 (6) | 24.8 (54) |
| 42 | 44.4 (3) | 30.1 (3) | 8.7 (14) |
| 44 | 40.0 (3) | 27.3 (3) | 5.8 (11) |
| 46 | 53.8 (6) | | 26.9 (52) |
| 49 | 50.0 (3) | 44.4 (4) | 15.5 (26) |
| 50 | | 55.6 (5) | 20.0 (24) |

* Number of genera.

State IV, a laterally directed lateral process of the palatine occurs in the following colubrids (plus other taxa):

Colubridae
- *Chilomeniscus cinctus*
- *Chilorhinophis carpenteri*
- *Dasypeltis inornatus*
- *Liodytes alleni*
- *Lycodon striatus*
- *Mehelya poensis*
- *Ninia sebae*
- *Oligodon octolineata*
- *Opisthoplus degener*
- *Oxyrhabdium modestum*
- *Phyllorhynchus decurtatus*
- *Rhadinaea seperaster*
- *Scaphiophis albopunctatus*
- *Tantilla gracilis*

Elapidae
- *Apistocalamus loriae*
- *Aspidomorphus lineaticollis*
- *Elapsoidea sundevalli*
- *Leptomicrurus collaris*
  - *narducci*
- *Micrurus affinis*
  - *fulvius*
  - *lemniscatus*
  - sp.
  - *spixi*
- *Toxicocalamus stanleyanus*

Hydrophiidae
- *Kolpophis annandalei*

In these colubrids this character state has a higher frequency of correlation with derived states of 11 other characters compared to the frequency distribution of these states of the same 11 characters in the total sample (table 83) (Criterion 3).

The colubrids also have a markedly larger number of species confined to the fossorial habitat (35.7 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent—table 84) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

From the distribution of states among the taxa it seems clear that the derivative states of the palatine process character are correlated with maximal mobility of the maxilla, palatine, or both. In the viperids, elapids, hydrophiids, and most aparallactine colubrids, the maxillary mobility is linked to the envenomation mechanism. In other colubrids, the nature of the food seems the paramount correlate: slugs and snails in the Dipsadinae (Peters, 1960 and *Tropidodipsas* (Scott, 1967)); bird eggs in *Dasypeltis* (Gans, 1952) and perhaps *Elachistodon* (Gans and Williams, 1954).

From the preceding it seems clear that State III, presence of a posteriorly directed process, is the primitive state among the colubrids. Intrageneric variation in the colubrids and the morphological relationship among States III, IV, and II (posterior, lateral, and anterior, respectively) suggest that shifts would ordinarily proceed in the order given. Ancillary evidence for a single direction of change from III to IV to II is furnished by the marked congruence of States IV and II in correlation with derived states of other characters (table 83) and in habitat distribution (table 84). That State II is the more derivative is indicated by its stronger and more numerous correlations in Table 83 and its more restricted variation among habitat types in Table 84. A more abrupt change in this sequence is possibly indicated in the hydrophiid genus *Laticauda*, where only States III and II are known. However, it is more likely that IV has merely dropped out within the genus.

TABLE 84. Habitat distribution of colubrid species having States II and IV of Character 29 compared to the total colubrid sample.

| | Total Working Sample | State II Character 29 | State IV Character 29 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | | 21.4 |
| Arboreal | 16.5 | 23.1 | 14.3 |
| Aquatic | 14.9 | | 7.1 |
| Subterrestrial | 10.8 | 30.8 | 14.3 |
| Fossorial | 12.4 | 46.2 | 35.7 |
| Variation | 5.3 | | |
| Unknown | 3.5 | | 7.1 |

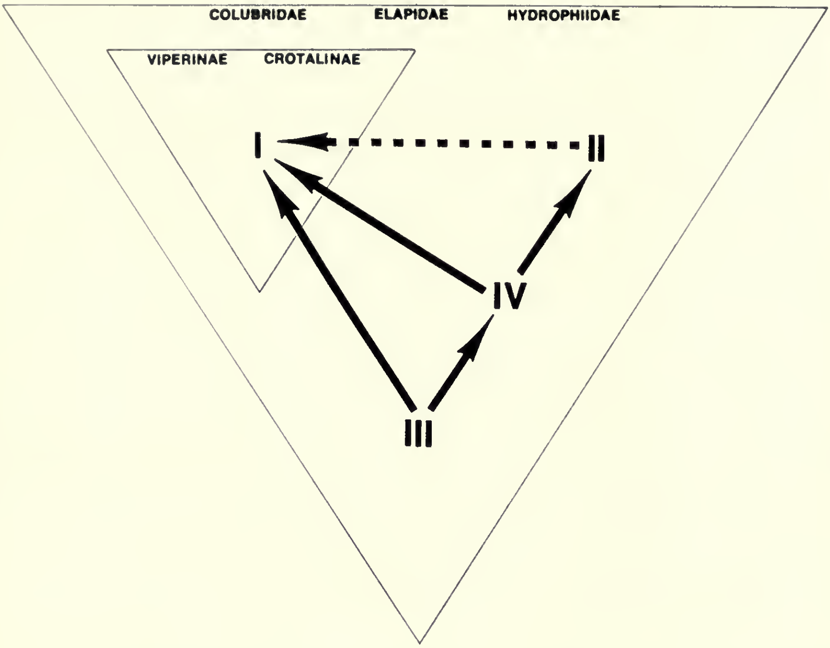

FIG. 28. Distribution among families of states of Character 29. Direction of change among states shown by arrows.

Lack of a process (State I) presumably stems from a prior state with a process. Intrageneric variation supports the notion that disappearance of the process could occur from States III and IV. Intrageneric evidence is wanting for a State II to State I transition, but that such occurred is suggested by the proportional distribution of states in the elapids (table 82) and the probable affinities of *Micropechis* (with an anterior process) to other New Guinean elapid taxa (without a process). We thus believe that State I could have arisen from any other state. There is no evidence to suggest the converse, nor an alternation of disappearance and reappearance. Our interpretations of the phyletics of Character 29 are summarized in Figure 28.

## Character 30—Maxillary Nerve Foramen In Palatine Bone

### DESCRIPTION OF CHARACTER

The palatine bone usually has a process situated on its lateral side (Character 29). When present this process almost always (exception in one species) has a foramen that passes through it near its base and along the body axis. This foramen is here referred to as the maxillary nerve foramen.

The lateral process of the palatine bone may be absent in some taxa (Character 29, State I). The absence of the maxillary nerve foramen is a necessary correlate in taxa lacking this process. Therefore we consider only taxa that have the lateral process of the palatine bone in the analysis of this foramen.

Three states are recognized:

State I —foramen absent

State II —foramen present

State III—intraspecific variation: both states I and II present (Colubridae: *Diadophis punctatus, Lamprophis aurora*) or incompletely walled foramen (Colubridae: *Helicops leopardinus*; Elapidae: *Micrurus affinis, Naja nivea*; Hydrophiidae: *Laticauda semifasciata, L. schistorhynchus*).

### FAMILIAL RANGES OF VARIATION (Table 85)

Colubridae—This family has all three states, plus the necessary correlate, in a sample of 287 species of 158 genera (531 skulls). State I occurs in 13 species of 12 genera (17 skulls), II in 269 species of 147 genera (499 skulls), III in 3 species of 3 genera (11 skulls). The necessary correlate occurs in 2 species of 2 genera (4 skulls).

Intrageneric variation occurs in 5 genera: one with States I, II, and III (*Diadophis*), one with States II and III (*Helicops*), two with States I and II (*Atractus, Lygophis*), and one with State I and the necessary correlate (*Tropidodipsas*).

Elapidae—This family has all three states, plus the necessary correlate, in a sample of 64 species of 35 genera (106 skulls). State I occurs in 15 species of 10 genera (18 skulls), II in 18 species of 12 genera (41 skulls), III in 2 species of 2 genera (4 skulls). The necessary correlate occurs in 29 species of 20 genera (43 skulls).

Intrageneric variation occurs in 6 genera: one with States I, II, and III (*Naja*), one with States I and III (*Micrurus*), two with State II and the necessary correlate (*Aspidelaps, Dendroaspis*), and two with State I and the necessary correlate (*Aspidomorphus, Denisonia*).

Hydrophiidae—The sea snakes have all three states, plus the necessary correlate, in a sample of 39 species of 15 genera (140 skulls).

TABLE 85. Distribution of character states of the maxillary nerve foramen in the lateral process of the palatine.

|  |  |  |  | Lateral Process of Palatine |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | STATES |  |  |  |  |  |  |  |  |  |
|  | II | III | I | nc[1] |  |  |  |  |  |  |
| Description | Present | Intraspecific Variation | Absent | Absent[1] |  |  |  |  |  |  |
|  | SPECIES[2] |  |  |  |  |  |  |  |  |  |
| Colubridae —287 | 93.7% | 1.0% | 4.5% | 0.7% |  |  |  |  |  |  |
| Elapidae — 64 | 28.1 | 3.1 | 23.4 | 45.3 |  |  |  |  |  |  |
| Hydrophiidae— 39 | 5.1 | 5.1 | 12.8 | 76.9 |  |  |  |  |  |  |
| Viperinae — 33 |  |  |  | 100.0 |  |  |  |  |  |  |
| Crotalinae — 43 |  |  |  | 100.0 |  |  |  |  |  |  |
| *Azemiops* — 1 |  |  |  | 100.0 |  |  |  |  |  |  |
| *Atractaspis* — 5 | 100.0 |  |  |  |  |  |  |  |  |  |
|  | GENERA |  |  |  | INTRAGENERIC VARIATION |  |  |  |  |  |
|  |  |  |  |  | II, III, I | II, III | II, I | III, I | II, nc | I, nc |
| Colubridae —158 | 90.5 | 0.6 | 5.1 | 0.6 | 0.6% | 0.6% | 1.3% |  |  | 0.6% |
| Elapidae — 35 | 22.9 |  | 14.3 | 45.7 | 2.9 |  |  | 2.9% | 5.7% | 5.7 |
| Hydrophiidae— 15 | 6.7 |  |  | 73.3 |  | 6.7 |  |  |  | 13.3 |
| Viperinae — 8 |  |  |  | 100.0 |  |  |  |  |  |  |
| Crotalinae — 6 |  |  |  | 100.0 |  |  |  |  |  |  |
| *Azemiops* — 1 |  |  |  | 100.0 |  |  |  |  |  |  |
| *Atractaspis* — 1 | 100.0 |  |  |  |  |  |  |  |  |  |

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[1] Necessary correlate of Character 29, State I.

[2] Working sample.

TABLE 86. Correlation of State I of Character 30 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters — | |
|---|---|---|
| | In species having State I of Character 30 | In total working sample |
| 7 | 61.5% (7) | 25.5% (56) |
| 19 | 61.5 (8) | 36.8 (68) |
| 32 | 50.0 (5) | 26.3 (55) |

State I occurs in 5 species of 3 genera (31 skulls), II in 2 species of *Laticauda* (12 skulls), III in the other 2 species of *Laticauda* (7 skulls). The necessary correlate occurs in 30 species of 13 genera (90 skulls).

Intrageneric variation occurs in 3 genera: one with States II and III (*Laticauda*) and two with State I and the necessary correlate (*Hydrophis, Lapemis*).

Viperinae, Crotalinae, *Azemiops*—These three taxa all have the necessary correlate in a sample of 77 species (33, 43, 1 respectively) of 15 genera (8, 6, 1) (178 skulls: 96, 80, 2).

*Atractaspis* has State II in a sample of 5 species (8 skulls).

### PHYLETICS OF CHARACTER 30

Character State I is rare in the colubrids (table 85) (Criterion 2). State I, absence of the maxillary nerve foramen in the lateral arm of the palatine, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Atractus ventrimaculatus*
  - *Diadophis amabilis*
  - *Dimades plicatilis*
  - *Duberria lutrix*
  - *Geophis multitorques*
  - *Lygophis boursieri*
  - *Manclepis putmani*
  - *Ninia atrata*
    - *sebae*
  - *Pseudorhabdion longiceps*
  - *Scaphiophis albopunctatus*
  - *Sibynomorphus turgidus*
  - *Tropidodipsas philippi*
- Elapidae
  - *Apistocalamus loriae*
  - *Denisonia par*
    - *woodfordi*
  - *Elaps lacteus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Maticora bivirgata*
  - *Micropechis elapsoides*
  - *Micruroides euryxanthus*
  - *Micrurus fulvius*
    - *lemniscatus*
    - sp.
    - *spixi*
  - *Naja flava*
  - *Toxicocalamus stanleyanus*
- Hydrophiidae
  - *Hydrophis brookii*
    - *klossi*
    - *torquatus*
  - *Kolpophis annandalei*
  - *Lapemis hardwickii*

In these colubrids this character state has a higher frequency of correlation with derived states of three other characters compared to the frequency distribution of these states of the same three characters in the total sample (table 86) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—77.0 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (table 87) (Criterion 5).

TABLE 87. Habitat distribution of colubrid species having State I of Character 30 compared to the total colubrid working sample.

| | Total Working Sample | State I Character 30 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 7.7 |
| Arboreal | 16.5 | 7.7 |
| Aquatic | 14.9 | 7.7 |
| Subterrestrial | 10.8 | 46.2 |
| Fossorial | 12.4 | 30.8 |
| Variation | 5.3 | |
| Unknown | 3.5 | |

Also there is a marked abundance of colubrid species from the New World—10 of 13, primarily from tropical America (9 of 10) (Criterion 6).

The application of four criteria (2, 3, 5, 6) suggests that this state is derived (Criterion 8).

State III is also very rare in colubrids. The colubrids (plus other taxa) having intraspecific variation are:

Colubridae
  *Diadophis punctatus*
  *Helicops leopardinus*
  *Lamprophis aurora*

Elapidae
  *Micrurus affinis*
  *Naja nivea*
Hydrophiidae
  *Laticauda schistorhynchus semifasciata*

State III is an intermediate sequential state because each taxon with this state either has both States I and II or has an intermediate morphological condition.

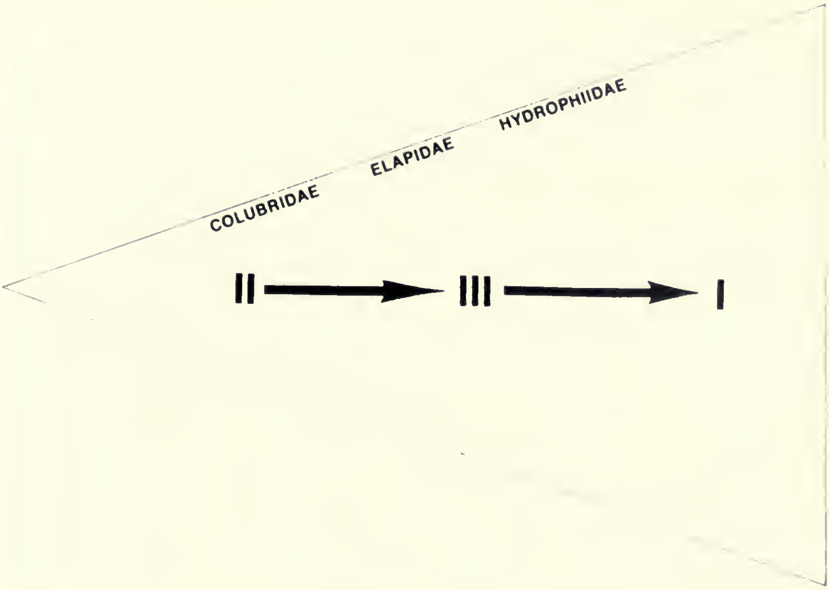

FIG. 29. Distribution among families of states of Character 30. Direction of change among states shown by arrows.

Our interpretation of the phyletics of Character 30 is shown in Figure 29.

## Character 31—Palatine-Pterygoid Articulation

### DESCRIPTION OF CHARACTER

Posteriorly the palatine bone is usually connected to the pterygoid along an antero-posterior axis. We here record the type of articulation the palatine has with the pterygoid.

Four states are recognized:

State I —overlap joint. There are various degrees of the positioning of these two bones, but basically the articular sections are parallel, in some cases forming an indenting union, but frequently they simply lie together in a syndesmotic plane joint.
State II —both bones notched, a saddle joint
State III—bones separated, not meeting each other (disjunct)
State IV—joint formed by a fossa in the palatine with a condylar head of pterygoid nestled within, i.e., "grooved"

TABLE 88. Distribution of character states of the palatine-pterygoid articulation.

| | STATES | | | | INTRAGENERIC VARIATION | | | |
|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | I, II | I, III | I, II, III | II, IV |
| Description | Overlap | Notched | Disjunct | Grooved | | | | |
| | | SPECIES[1] | | | | | | |
| Colubridae —298 | 80.5% | 18.1% | 1.3% | | | | | |
| Elapidae — 65 | 44.6 | 35.4 | 15.4 | 4.6% | | | | |
| Hydrophiidae— 42 | 76.2 | 23.8 | | | | | | |
| Viperinae — 33 | 97.0 | 3.0 | | | | | | |
| Crotalinae — 45 | 11.1 | 88.9 | | | | | | |
| *Azemiops* — 1 | | 100.0 | | | | | | |
| *Atractaspis* — 5 | | | 100.0 | | | | | |
| | | GENERA | | | | | | |
| Colubridae —161 | 72.7 | 19.9 | 2.5 | | 5.0% | | | |
| Elapidae — 38 | 42.1 | 34.2 | 13.2 | 2.6 | | 2.6% | 2.6% | 2.6% |
| Hydrophiidae— 16 | 62.5 | 37.5 | | | | | | |
| Viperinae — 8 | 87.5 | | | | 12.5 | | | |
| Crotalinae — 6 | | 83.3 | | | 16.7 | | | |
| *Azemiops* — 1 | | 100.0 | | | | | | |
| *Atractaspis* — 1 | | | 100.0 | | | | | |

[1] Working sample.

### FAMILIAL RANGES OF VARIATION (Table 88)

Colubridae—This family has States I, II, and III in a sample of 298 species of 161 genera (553 skulls). State I occurs in 240 species of 125 genera (462 skulls), II in 54 species of 40 genera (86 skulls), III in 4 species of 4 genera (5 skulls).

Intrageneric variation occurs in eight genera: *Alsophis, Boiga, Enhydris, Lystrophis, Malpolon, Pseudoboa, Telescopus,* and *Xenodon* have States I and II.

Elapidae—This family has all four states in a sample of 65 species of 38 genera (107 skulls). State I occurs in 29 species of 18 genera (55 skulls), II in 23 species of 15 genera (35 skulls), III in 10 species of 7 genera (14 skulls), IV in 3 species of 2 genera (3 skulls).

Intrageneric variation occurs in three genera: *Micrurus* (I, III), *Naja* (I, II, III), and *Denisonia* (II, IV).

Hydrophiidae—The sea snakes have States I and II in a sample of 42 species of the 16 genera (143 skulls). State I occurs in 32 species of 10 genera (107 skulls), II in 10 species of 6 genera (36 skulls).

Viperinae—The true vipers have States I and II in a sample of 33 species of the 8 genera (94 skulls). State I occurs in 32 species of the 8 genera (93 skulls), II in *Atheris superciliaris* (1 skull).

Intrageneric variation occurs in *Atheris.*

Crotalinae—The pit vipers have States I and II in a sample of 45 species of the 6 genera (82 skulls). State I occurs in 5 species of *Agkistrodon* (5 skulls), II in 40 species of the 6 genera (77 skulls).

Intrageneric variation occurs in *Agkistrodon.*

*Azemiops* has State II (2 skulls).

*Atractaspis* has State III in a sample of 5 species (8 skulls).

### PHYLETICS OF CHARACTER 31

Character State II is not particularly rare in the colubrids (table 88).

State II, a notched joint, occurs in the following colubrids (plus other taxa):

Colubridae
- *Abastor erythrogrammus*
- *Alsophis sanctae-crucis*
- *Apostolepis ambinigra*
- *Arizona elegans*
- *Aspidura trachyprocta*
- *Boaedon lineatus*
- *Boiga blandingi*
  - *cynodon*
  - *dendrophila*
  - *irregularis*
  - *kraepelini*
  - *multimaculata*

- *pulverulentus*
- *trigonatus*
- *Crotaphopeltis hotamboeia*
- *Cyclocorus lineatus*
- *Dimades plicatilis*
- *Dipsadoboa unicolor*
- *Dromicodryas bernieri*
- *Enhydris bocourti*
  - *enhydris*
  - *plumbea*
- *Ficimia publia*
- *Grayia smithi*
- *Holarchus formosanus*
  - *hainanensis*
  - *violaceus*
- *Hydraethiops melanogaster*
- *Hypsirhynchus ferox*
- *Liodytes alleni*
- *Lystrophis d'orbignyi*
- *Macropisthodon rudis*
- *Malpolon moilensis*
- *Manolepis putmani*
- *Mimophis mahfalensis*
- *Opisthoplus degener*
- *Oxyrhopus petola*
- *Psammodynastes pictus*
  - *pulverulentus*
- *Psammophylax rhombeatus*
- *Pseudaspis cana*
- *Pseudoboa clathrata*
- *Pythonodipsas carinata*
- *Scaphiophis albopunctatus*
- *Siphlophis cervinus*
- *Spalerosophis diadema*
- *Stilostoma extenuatum*
- *Tachymenis chilensis*
  - *peruviana*
- *Telescopus semiannulatus*
- *Tripanurgos compressus*
- *Uromacer catesbyi*
  - *oxyrhynchus*
- *Xenodon merremii*

Elapidae
- *Acanthophis antarcticus*
- *Aspidomorphus lineaticollis*
  - *muelleri*
- *Boulengerina annulata*
- *Demansia olivacea*
  - *textilis*
- *Denisonia coronoides*
  - *fasciata*
  - *nigrescens*
  - *superba*
- *Elapognathus minor*
- *Glyphodon tristis*
- *Micropechis elapsoides*
  - *ikaheka*
- *Naja flava*
- *Notechis scutatus*
- *Oxyuranus scutellatus*
- *Parapistocalamus hedigeri*
- *Pseudechis australis*
  - *papuanus*
  - *porphyriacus*
- *Rhynchoelaps bertholdi*
- *Vermicella annulata*

Hydrophiidae
- *Ephalophis*
- *Hydrelaps*
- *Kolpophis*
- *Lapemis*
- *Laticauda*
- *Thalassophis*

Viperinae
- *Atheris superciliaris*

Crotalinae
- *Agkistrodon acutus*
  - *contortrix*
  - *halys*
  - *piscivorus*
- *Bothrops*
- *Crotalus*
- *Lachesis*
- *Sistrurus*
- *Trimeresurus*

*Azemiops*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 89) (Criterion 3).

TABLE 89. Correlation of State II of Character 31 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State II of Character 31 | | In total working sample | |
| 1 | 24.1% | (11)* | 14.3% | (28) |
| 4 | 16.7 | (2) | 3.8 | (4) |
| 9 | 11.8 | (6) | 6.8 | (14) |
| 21 | 30.0 | (7) | 18.9 | (29) |
| 41 | 22.6 | (7) | 10.9 | (20) |
| 46 | 52.8 | (18) | 26.9 | (52) |

* Number of genera.

These colubrids also have a markedly larger number of species confined to the arboreal habitat (27.8 per cent) compared to the relative abundance of arboreal species in the total sample (16.5 per cent—table 90) (Criterion 5).

The application of two criteria (3, 5) suggests that this state is derived (Criterion 8).

Character State III is very rare in the colubrids (table 88) (Criterion 2).

TABLE 90. Habitat distribution of colubrid species having State II of Character 31 compared to the total colubrid working sample.

| | Total Working Sample | State II Character 31 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 38.9 |
| Arboreal | 16.5 | 27.8 |
| Aquatic | 14.9 | 13.0 |
| Subterrestrial | 10.8 | 9.3 |
| Fossorial | 12.4 | 7.4 |
| Variation | 5.3 | 3.7 |
| Unknown | 3.5 | |

State III, bones disjunct, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Aparallactus werneri*
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Miodon gabonensis*
- Elapidae
  - *Aspidelaps lubricus*
  - *Elaps lacteus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Micruroides euryxanthus*
  - *Micrurus fulvius*
    - *spixi*
  - *Naja nigricollis*
  - *Ultrocalamus preussi*
- *Atractaspis*

All of the above colubrids belong to the Aparallactinae (Criterion 7) and are burrowers from tropical Africa (Inger and Marx, 1965; Kochva et al., 1967). Also all these species have only derived states for Characters 7, 19, 34, 36, and 37 (Criterion 3).

We believe this state reflects a single origin for these forms since this group has so rare a character state (Criterion 2), are all from one geographic range (Criterion 6), and occupy a single habitat zone (Criterion 5).

Obviously redundancy of criteria occurs here. In having a closely related group of taxa, it follows that these animals most likely will occupy the same sorts of habitats in a restricted geographic range and function in much the same ways. However this still reflects a derived condition for this state and in the colubrids it is highly unlikely that there is convergence in this character state.

It appears that the overlap joint (I) is functionally less complicated than the notched joint (II) and the grooved joint (IV). Therefore the disjunct condition (III) probably arose from the least complicated joint (I), which involves much less morphological and functional adjustment to change into a disconnected condition.

The only "vipers" having the palatine not attached to the pterygoid are the species of the genus *Atractaspis*. *Atractaspis* species are also burrowers from tropical Africa. Therefore it is likely that this character state reflects the relationship of *Atractaspis* with the Aparallactinae proposed by Bourgeois (1965), Kochva et al. (1967), and McDowell (1968).

Character State IV does not occur in the colubrids and rarely occurs in the derived elapids. We apply the uniqueness criterion (1) to Character State IV, for its presence is unique to a derived stock.

The elapids having State IV, a grooved joint, are *Denisonia par*, *D. woodfordi*, and *Ogmodon vitianus*. Klemmer (1963, p. 293) considers *D. woodfordi* a subspecies of *D. par*. The state may have arisen once for it is present in so few taxa of the New-Guinean-Solomon Ids.-Fiji Ids. region. The genus *Denisonia* is considered a polyphyletic composite (McDowell, 1967, p. 536) and we may have some reflection of close relationship between "*D.*" *par* and *Ogmodon*.

We believe that the two morphologically more complex joints (II, IV) arose from the less complex joint (I). Genetically and morphologically it is probably much less complicated to evolve from jointed bones than from a disjunct condition of two bones. We also suggest that these two types of joints each arose directly from the less

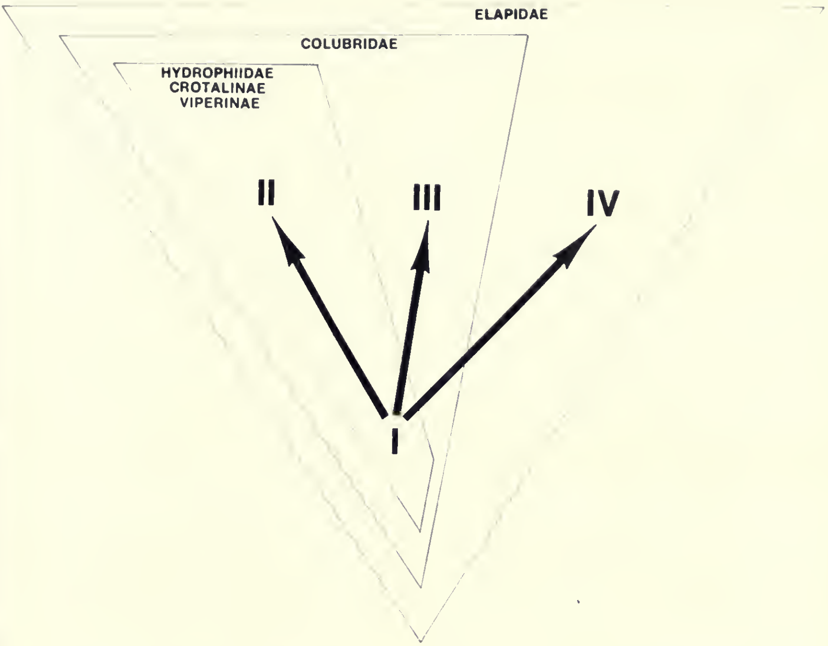

FIG. 30. Distribution among families of states of Character 31. Direction change among states shown by arrows.

complicated joint and not each other, for these two joints are very distinct from each other, not representing a progression of morphological similarity.

Our interpretation of the phyletics of Character 31 is shown in Figure 30.

## Character 32—Medial Wing of Prefrontal

### DESCRIPTION OF CHARACTER

The prefrontal bone usually has a thin vertical bony process situated anteroventrally above the lacrimal canal. The process can best be seen by viewing the skull frontally. It has been termed the nasal process by Duellman (1958). In its fullest expression the process is expanded distally, and we thus term it a "wing."

Three states are recognized:

State I —wing absent
State II —wing present
State III—wing present, but small in size

TABLE 91. Distribution of character states of the antero-ventral-medial wing of the prefrontal.

| | STATES | | | VARIATION | | | |
|---|---|---|---|---|---|---|---|
| | II | III | I | | | | |
| Description | Present | Present & Reduced | Absent | III, II | III, I | II, I | II, III, I |
| | | SPECIES[1] | | | | | |
| Colubridae —266 | 73.7% | 9.8% | 16.5% | | | | |
| Elapidae — 51 | 41.2 | 21.6 | 37.3 | | | | |
| Hydrophiidae— 42 | | | 100.0 | | | | |
| Viperinae — 34 | | 8.8 | 88.2 | | 2.9% | | |
| Crotalinae — 44 | | 20.5 | 79.5 | | | | |
| *Azemiops* — 1 | 100.0 | | | | | | |
| *Atractaspis* — 5 | | | 100.0 | | | | |
| | | GENERA | | | | | |
| Colubridae —152 | 63.2 | 9.2 | 20.4 | 3.3% | 1.3 | 2.0% | 0.7% |
| Elapidae — 32 | 34.4 | 9.4 | 37.5 | 3.1 | 12.5 | | 3.1 |
| Hydrophiidae— 16 | | | 100.0 | | | | |
| Viperinae — 8 | | 12.5 | 75.0 | | | | 12.5 |
| Crotalinae — 6 | | 16.7 | 33.3 | | 50.0 | | |
| *Azemiops* — 1 | 100.0 | | | | | | |
| *Atractaspis* — 1 | | | 100.0 | | | | |

[1] Working sample.

## Familial Ranges of Variation (Table 91)

Colubridae—This family has all three states in a sample of 266 species of 152 genera (518 skulls). State I occurs in 44 species of 36 genera (73 skulls), II in 196 species of 106 genera (401 skulls), III in 26 species of 21 genera (44 skulls).

Ten genera have intrageneric variation: four genera (*Arrhyton, Helicops, Rhadinaea, Salvadora*) have the wing present or reduced—States II and III; two genera (*Lygophis, Malpolon*) have the wing present or absent—States I and II; two genera (*Dromophis, Lytorhynchus*) have the wing reduced or absent—States I and III; two genera (*Alsophis, Enhydris*) have all three states.

Elapidae—This family has all three states in a sample of 51 species of 32 genera (92 skulls). State I occurs in 19 species of 17 genera (22 skulls), II in 21 species of 13 genera (48 skulls), III in 11 species of 9 genera (24 skulls).

Intrageneric variation occurs in six genera: one genus (*Denisonia*) has the wing present or reduced—States II and III; 4 genera (*Hoplocephalus, Micrurus, Pseudechis, Pseudohaje*) have the wing reduced or absent— States I and III; one genus (*Naja*) has all three states.

Hydrophiidae—The sea snakes only have State I in a sample of 42 species of the 16 genera (143 skulls).

Viperinae—The true vipers have States I and III in a sample of 34 species of the 8 genera (93 skulls). State I occurs in 30 species of 7 genera (77 skulls), III in 3 species of 2 genera (11 skulls).

Intrageneric variation occurs in *Vipera,* which have the wing reduced and absent. In a single species (*Vipera russelii*—7 skulls) we observed intraspecific variation with States I and III.

Crotalinae—The pit vipers have States I and III in a sample of 44 species of the 6 genera (80 skulls). State I occurs in 35 species of 5 genera (65 skulls), III in 9 species of 4 genera (15 skulls).

Intrageneric variation (I and III) occurs in three genera (*Bothrops, Crotalus, Trimeresurus*).

*Azemiops* has State II (2 skulls).

*Atractaspis* has State II in a sample of 5 species (8 skulls).

## Phyletics of Character 32

Character State I is not particularly rare in the colubrids (table 91). State I, absence of the anteroventral medial wing, occurs in the following colubrids (plus other taxa):

Colubridae
- *Alsophis sanctae-crucis*
- *Apostolepis ambinigra*
- *Arizona elegans*
- *Aspidura trachyprocta*
- *Atractus elaps*
  - *erythromelas*
  - *latifrons*
  - *ventrimaculatus*
- *Brachyorrhus albus*
- *Calamaria septentrionalis*
- *Calamelaps unicolor*
- *Cemophora coccinea*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Chilorhinophis carpenteri*
- *Chionactis occipitalis*
- *Conopsis lineatus*
  - *nasus*
- *Dimades plicatilis*
- *Dromophis lineatus*
- *Drymobius margaritiferus*
- *Enhydris enhydris*
- *Farancia abacura*
- *Ficimia publia*
- *Homalopsis buccata*
- *Hydraethiops melanogaster*
- *Hydrops triangularis*
- *Lycophidion capense*
- *Lygophis flavifrenatus*
- *Lytorhynchus maynardi*
- *Malpolon moilensis*
- *Manolepis putmani*
- *Miodon gabonensis*
- *Oxyrhabdium modestum*
- *Passerita mycterizans*
  - *nasuta*
  - *prasinus*
- *Prosymna ambigua*
- *Pseudorhabdion longiceps*
- *Rhamphiophis oxyrhynchus*
- *Sonora episcopa*
  - *semiannulata*
- *Tantilla gracilis*
- *Tretanorhinus variabilis*

- Elapidae
  - *Apistocalamus loriae*
  - *Aspidelaps lubricus*
  - *Aspidomorphus lineaticollis*
  - *Boulengerina annulata*
  - *Brachyurophis semifasciata*
  - *Cacophis harriettae*
  - *Elaps lacteus*
  - *Hoplocephalus bitorquatus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Maticora bivirgata*
  - *Micruroides euryxanthus*
  - *Micrurus fulvius*
    - *lemniscatus*
  - *Naja naja*
  - *Pseudechis porphyriacus*
  - *Pseudohaje nigra*
  - *Toxicocalamus stanleyanus*
  - *Walterinnesia aegyptia*
- Hydrophiidae (all taxa)
- Viperinae
  - *Adenorhinos*
  - *Atheris*
  - *Bitis*
  - *Causus*
  - *Cerastes*
  - *Eristicophis*
  - *Vipera ammodytes*
    - *aspis*
    - *berus*
    - *latasti*
    - *lebetina*
    - *persica*
    - *ursini*
- Crotalinae
  - *Agkistrodon*
  - *Bothrops alternatus*
    - *atrox*
    - *barnetti*
    - *cotiara*
    - *dunni*
    - *lansbergii*
    - *nummifer*
    - *schlegeli*
  - *Crotalus adamanteus*
    - *atrox*
    - *basiliscus*
    - *cerastes*
    - *durissus*
    - *horridus*
    - *lepidus*
    - *mitchelli*
    - *molossus*
    - *pusillus*
    - *ruber*
  - *Lachesis*
  - *Trimeresurus albolabris*
    - *monticola*
    - *puniceus*
    - *stejnegeri*
    - *sumatranus*
    - *wagleri*

*Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total sample (table 92) (Criterion 3).

These colubrids also have a markedly larger number of species confined to secretive habitats (subterrestrial and fossorial—63.7 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (table 93) (Criterion 5).

The application of two criteria (3, 5) suggests that this state is derived (Criterion 8).

State III is rare in the colubrids (table 91) (Criterion 2).

State III, a reduced wing, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Alsophis dorsalis*
  - *Arrhyton vittatum*
  - *Coniophanes fissidens*
  - *Darlingtonia haetiana*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Dromophis praeornata*
  - *Duberria lutrix*
  - *Enhydris bocourti*
    - *chinensis*
  - *Helicops leopardinus*
  - *Hypsirhynchus ferox*
  - *Leimadophis melanotus*
    - *reginae*
  - *Lystrophis d'orbignyi*
  - *Lytorhynchus diadema*
  - *Pythonodipsas carinata*
  - *Rhacidelus brazili*
  - *Rhidinaea brevirostris*
  - *Rhamnophis aethiopissa*
  - *Rhinocheilus lecontei*
  - *Rhinostoma guianense*
  - *Salvadora hexalepis*
  - *Simophis rhinostoma*
  - *Stilostoma extenuatum*
- Elapidae
  - *Brachyaspis curta*
  - *Calliophis japonicus*
  - *Denisonia coronoides*
  - *Elapognathus minor*
  - *Hoplocephalus bungaroides*
  - *Micrurus* sp.
    - *spixi*
  - *Naja melanoleuca*
    - *nivea*
  - *Pseudechis papuanus*
  - *Pseudohaje goldii*
- Viperinae
  - *Echis*
  - *Vipera xanthina*
- Crotalinae
  - *Bothrops godmanni*
    - *neuwiedi*
  - *Crotalus viridis*
  - *Sistrurus*
  - *Trimeresurus flavoviridis*
    - *jerdoni*
    - *mucrosquamatus*
    - *okinavensis*

TABLE 92. Correlation of State I of Character 32 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State I of Character 32 | | In total working sample | |
| 1 | 34.1% | (14)* | 14.3% | (28) |
| 2 | 36.4 | (12) | 15.6 | (31) |
| 5 | 13.6 | (5) | 3.5 | (9) |
| 7 | 50.0 | (17) | 25.5 | (56) |
| 9 | 15.9 | (7) | 6.8 | (14) |
| 14 | 11.4 | (3) | 3.5 | (7) |
| 19 | 59.1 | (21) | 36.8 | (68) |
| 22 | 15.9 | (7) | 4.5 | (11) |
| 25 | 16.7 | (5) | 6.3 | (12) |
| 29 | 23.1 | (8) | 10.1 | (27) |
| 31 | 33.3 | (13) | 19.5 | (44) |
| 34 | 25.0 | (9) | 6.8 | (18) |
| 36 | 18.6 | (8) | 6.1 | (16) |
| 39 | 23.3 | (7) | 9.0 | (15) |
| 40 | 44.2 | (15) | 24.8 | (54) |
| 42 | 36.0 | (7) | 8.7 | (14) |
| 46 | 41.9 | (16) | 26.9 | (52) |

* Number of genera.

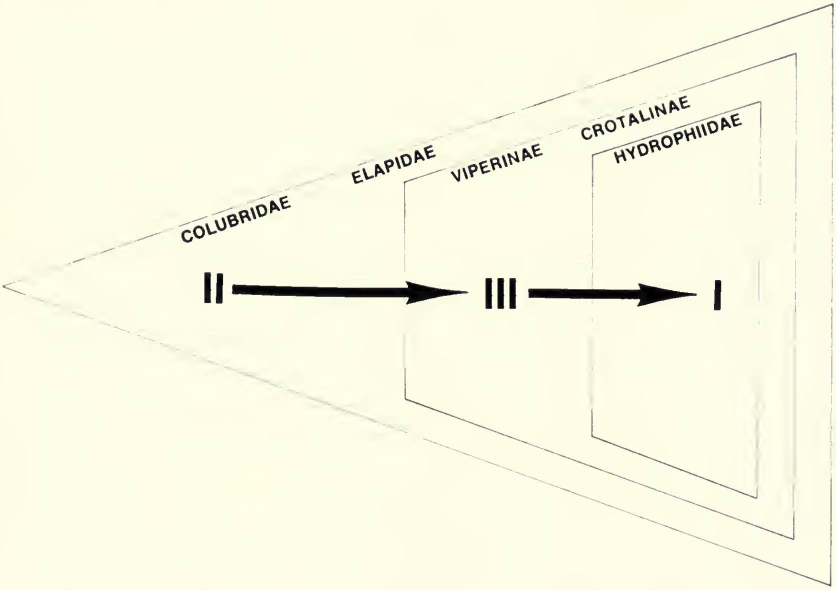

FIG. 31. Distribution among families of states of Character 32. Direction of change among states shown by arrows.

State III is an intermediate sequential state because it is an intermediate morphological condition between States I and II. This decision is reinforced by the intrageneric variation that occurs: two-thirds (9 of the 15) of the genera having small wings also have member species with the wing absent; in addition there is intraspecific variation in *Vipera russelii,* in which our sample of seven skulls shows a very small process in some specimens and none at all in others.

Our interpretation of the phyletics of Character 32 is shown in Figure 31.

TABLE 93. Habitat distribution of colubrid species having State I of Character 32 compared to the total colubrid working sample.

| | Total Working Sample % | State I Character 32 % |
|---|---|---|
| Terrestrial | 36.2 | 13.6 |
| Arboreal | 16.5 | 9.1 |
| Aquatic | 14.9 | 13.6 |
| Subterrestrial | 10.8 | 20.5 |
| Fossorial | 12.4 | 43.2 |
| Variation | 5.3 | |
| Unknown | 3.5 | |

## Character 33—Dorsal Processes of Prefrontal

### DESCRIPTION OF CHARACTER

The prefrontal bone articulates dorsally with the frontal. When viewed dorsally the prefrontal may have various processes, usually flat and abutting the anterior or lateral edges of the frontal.

Five states are recognized:

State I —no processes
State II —medial dorsal process
State III—posterior dorsal process
State IV—medial and posterior dorsal processes
State V —short, knobby processes engaging similar frontal structures in loose joint

### FAMILIAL RANGES OF VARIATION (Table 94)

Colubridae—This family has four states in a sample of 307 species of 172 genera (565 skulls). State I occurs in 175 species of 97 genera (319 skulls), II in 112 species of 65 genera (215 skulls), III occurs in 12 species of 9 genera (17 skulls), IV occurs in 7 species of 4 genera (12 skulls).

Intraspecific variation occurs in *Tachymenis peruviana* (I, II).

Intrageneric variation occurs in 14 genera: *Boiga, Elaphe, Helicops, Lygophis, Malpolon, Natrix, Oxybelis, Rhadinaea, Tachymenis, Tropidodipsas, Xenodon* (I, II), *Enhydris* (II, IV), *Holarchus* (I, II, IV), *Lycodon* (I, III).

Elapidae—This family has four states in a sample of 67 species of 37 genera (109 skulls). State I occurs in 5 species of 3 genera (8 skulls), II in 38 species of 19 genera (67 skulls), III in 18 species of 15 genera (26 skulls), IV in 6 species of 6 genera (8 skulls).

Intrageneric variation occurs in seven genera: *Aspidelaps, Demansia* (II, III); *Micropechis* (II, IV); *Denisonia* (I, II, III); *Aspidomorphus, Hoplocephalus, Pseudechis* (III, IV).

Hydrophiidae—The sea snakes have States II, III, and IV in a sample of 42 species of the 16 genera (143 skulls). State II occurs in 6 species of 5 genera (20 skulls), III in 33 species of 13 genera (112 skulls), IV in 3 species of 2 genera (11 skulls).

Intrageneric variation occurs in three genera: *Microcephalophis* (II, III); *Laticauda* (II, IV); *Hydrophis* (II, III, IV).

TABLE 94. Distribution of character states of the dorsal processes of the prefrontal.

| | | STATES | | | | |
|---|---|---|---|---|---|---|
| | | I | II | III | IV | V |
| Description | | Absent | Medial | Posterior | Medial & Posterior | Short Knobby |
| | | | | SPECIES | | |
| Colubridae | —307* | 57.0% | 36.5% | 3.9% | 2.3% | |
| Elapidae | — 67 | 7.5 | 56.7 | 26.9 | 9.0 | |
| Hydrophiidae | — 42 | | 14.3 | 78.6 | 7.1 | |
| Viperinae | — 34 | | 85.3 | | 14.7 | |
| Crotalinae | — 45 | | | | | 100.0% |
| *Azemiops* | — 1 | | | | 100.0 | |
| *Atractaspis* | — 5 | | | | 100.0 | |
| | | | | GENERA | | |
| Colubridae | —172 | 50.0 | 36.0 | 4.7 | 1.2 | |
| Elapidae | — 37 | 5.4 | 43.2 | 27.0 | 5.4 | |
| Hydrophiidae | — 16 | | 12.5 | 68.8 | | |
| Viperinae | — 8 | | 87.5 | | 12.5 | |
| Crotalinae | — 6 | | | | | 100.0 |
| *Azemiops* | — 1 | | | | 100.0 | |
| *Atractaspis* | — 1 | | | | 100.0 | |

INTRAGENERIC VARIATION (%)

| | I, II | I, III | I, II, III | I, II, IV | II, III | II, IV | II, III, IV | III, IV |
|---|---|---|---|---|---|---|---|---|
| Colubridae | 6.4 | 0.6 | | 0.6 | | 0.6 | | |
| Elapidae | | | 2.7 | | 5.4 | 2.7 | | 8.1 |
| Hydrophiidae | | | | | 6.3 | 6.3 | 6.3 | |

* Intraspecific variation in Colubridae = 0.3.

TABLE 95. Correlation of States I and II of Character 33 with derived states of the other characters in Colubridae.

| Character | Frequency of derived states in indicated characters— | | | Character | Frequency of derived states in indicated characters— | | |
|---|---|---|---|---|---|---|---|
| | In species having State I of Character 33 | In species having State II of Character 33 | In total working sample | | In species having State I of Character 33 | In species having State II of Character 33 | In total working sample |
| 1 | 15.4% (17)* | 8.9% (7) | 14.3% (28) | 26 | 7.3% (9) | 18.1% (11) | 12.6% (19) |
| 2 | 16.6 (21) | 15.2 (7) | 15.6 (31) | 27 | 17.4 (21) | 17.5 (16) | 17.9 (40) |
| 3 | 0.6 (1) | 0.9 (1) | 0.1 (3) | 28 | 10.3 (11) | 10.0 (8) | 11.7 (26) |
| 4 | 1.1 (2) | 8.0 (2) | 3.8 (4) | 29 | 7.8 (11) | 5.6 (6) | 10.1 (27) |
| 5 | 5.1 (8) | 0 | 3.5 (9) | 30 | 6.8 (10) | 2.0 (2) | 6.3 (15) |
| 6 | 0 | 0 | 0 | 31 | 16.0 (25) | 18.9 (14) | 19.5 (44) |
| 7 | 27.4 (31) | 17.9 (17) | 25.5 (56) | 32 | 31.1 (37) | 14.4 (11) | 26.3 (55) |
| 8 | 0 | 0 | 0 | 34 | 6.1 (9) | 2.8 (3) | 6.8 (18) |
| 9 | 6.4 (7) | 4.5 (3) | 6.8 (14) | 35 | 2.3 (4) | 0.9 (1) | 2.0 (6) |
| 10 | 0 | 0 | 0.6 (1) | 36 | 4.6 (7) | 4.5 (4) | 6.1 (16) |
| 11 | 24.6 (22) | 32.4 (23) | 26.7 (50) | 37 | 25.7 (34) | 17.0 (15) | 22.9 (54) |
| 12 | 3.4 (6) | 6.3 (5) | 4.8 (13) | 38 | 14.8 (15) | 17.7 (10) | 16.2 (27) |
| 13 | 27.9 (27) | 39.3 (24) | 31.8 (54) | 39 | 8.1 (7) | 3.7 (3) | 9.0 (15) |
| 14 | 2.9 (3) | 2.7 (2) | 3.5 (7) | 40 | 20.0 (28) | 32.1 (22) | 24.8 (54) |
| 15 | 0 | 0 | 0 | 41 | 12.0 (12) | 8.6 (6) | 10.9 (20) |
| 16 | 27.4 (22) | 14.3 (11) | 21.7 (34) | 42 | 11.0 (10) | 1.4 (1) | 8.7 (14) |
| 17 | 33.5 (24) | 39.3 (24) | 35.4 (48) | 43 | 1.2 (2) | 0 | 1.9 (3) |
| 18 | 1.7 (1) | 0 | 0.1 (3) | 44 | 6.5 (6) | 3.6 (3) | 5.8 (11) |
| 19 | 28.5 (35) | 41.5 (26) | 36.8 (68) | 45 | 10.6 (5) | 30.4 (13) | 19.5 (21) |
| 20 | 42.9 (42) | 37.8 (28) | 41.2 (74) | 46 | 20.1 (28) | 32.7 (20) | 26.9 (52) |
| 21 | 15.9 (15) | 22.7 (15) | 18.9 (29) | 47 | 54.4 (60) | 42.3 (47) | 48.5 (84) |
| 22 | 4.6 (6) | 2.7 (2) | 4.5 (11) | 48 | 7.2 (7) | 5.9 (4) | 6.2 (11) |
| 23 | 1.1 (2) | 3.6 (3) | 1.9 (5) | 49 | 17.2 (18) | 11.1 (7) | 15.5 (26) |
| 24 | 3.4 (6) | 2.7 (3) | 3.8 (11) | 50 | 22.2 (17) | 15.7 (7) | 20.0 (24) |
| 25 | 5.6 (6) | 6.0 (4) | 6.3 (12) | | | | |

* (number of genera)

Viperinae—The true vipers have States II and IV in a sample of 34 species of the 8 genera (95 skulls). State II occurs in 29 species of 7 genera (84 skulls), IV in 5 species of *Causus* (11 skulls).

Crotalinae—The pit vipers only have State V in a sample of 45 species of the 6 genera (82 skulls).

*Azemiops* has State IV (2 skulls).

*Atractaspis* has State IV in a sample of 5 species (8 skulls).

## PHYLETICS OF CHARACTER 33

Character States I and II are both common in the colubrids (57.0 per cent and 36.5 per cent—table 94). These colubrid species, having either States I or II, do not have a high frequency of correlation with any derived states of the 49 other characters in the total sample (table 95).

Also both these states do not have a significantly larger number of species confined to a particular geographic range compared to the relative abundance of colubrid species in the total sample (table 96).

In addition colubrid species having State I do not have a significantly larger number of species confined to any particular habitat

TABLE 96. Geographic distribution of colubrid species having States I, II, III, and IV of Character 33 compared to the total colubrid sample.

| | Total working sample | STATES | | | |
|---|---|---|---|---|---|
| | | I | II | III | IV |
| United States | 17.2% | 19.4% | 16.1% | | 14.3% |
| South America | 17.8 | 17.7 | 18.8 | 16.7% | |
| Central America | 6.7 | 6.3 | 8.0 | | |
| Mexico | 7.0 | 8.0 | 8.0 | | |
| Caribbean | 3.5 | 6.3 | | | |
| New World, intraregional | 1.9 | 2.3 | 1.8 | | |
| Tropical Africa | 14.3 | 11.4 | 15.2 | 58.3 | |
| Northern Africa & Sahara | 1.3 | 1.7 | 0.9 | | |
| Europe | 1.6 | 2.9 | | | |
| Southwestern Asia to Pakistan | 2.5 | 3.4 | 1.8 | | |
| India, Ceylon, Nepal | 2.9 | 0.6 | 2.7 | 8.3 | 14.3 |
| Eastern Asia | 10.8 | 10.9 | 9.8 | | 57.1 |
| Southeastern Asia | 1.9 | 1.1 | 3.6 | | |
| Indo-Australia-Phil. Ids. | 4.8 | 3.4 | 5.4 | 16.7 | |
| Moluccan | 0.6 | 0.6 | 0.9 | | |
| New Guinea-New Britain | 0.6 | 0.6 | 0.9 | | |
| Madagascar | 1.3 | 1.7 | 0.9 | | |
| Old World, intraregional | 3.2 | 1.7 | 5.4 | | 14.3 |
| Total number species* | 314 | 175 | 112 | 12 | 7 |

* Data on this character lacking on 6 species and 1 species with intraspecific variation.

TABLE 97. Habitat distribution of colubrid species having States I, II, III, and IV of Character 33 compared to the total colubrid sample.

| | Total working sample | CHARACTER 33 STATES | | | |
|---|---|---|---|---|---|
| | | I | II | III | IV |
| Terrestrial | 36.2% | 42.3% | 28.6% | 33.3% | 28.6% |
| Arboreal | 16.5 | 9.7 | 31.3 | | |
| Aquatic | 14.9 | 14.9 | 13.4 | 8.3 | 57.1 |
| Subterrestrial | 10.8 | 10.3 | 9.8 | 16.7 | 14.3 |
| Fossorial | 12.4 | 16.6 | 1.8 | 41.7 | |
| Variation | 5.3 | 1.7 | 13.4 | | |
| Unknown | 3.5 | 4.6 | 1.8 | | |

zone compared to the relative abundance of colubrid species in the total sample (table 97). However, State II has a markedly larger number of species confined to the arboreal habitat (31.3 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent) (table 97) (Criterion 5).

We conclude that since there are no criteria applicable to State I, this state is primitive. It follows that State II is a derived state because a single criterion is applicable.

State II, presence of a medial dorsal process of the prefrontal, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Aspidura trachyprocta*
  - *Boiga blandingi*
    - *cynodon*
    - *dendrophila*
    - *jaspidea*
    - *kraepelini*
    - *multimaculata*
    - *pulverulentus*
    - *trigonatus*
  - *Coniophanes fissidens*
  - *Crotaphopeltis hotamboeia*
  - *Cryophis hallbergi*
  - *Cyclagras gigas*
  - *Dipsadoboa unicolor*
  - *Dispholidus typus*
  - *Drymarchon corais*
  - *Dryocalamus davisoni*
  - *Dugandia bicolor*
  - *Elaphe frenatus*
  - *Enhydris bocourti*
  - *Erythrolamprus aesculapii*
  - *Gastropyxis smaragdina*
  - *Haldea striatula*
    - *valeriae*
  - *Hapsidophrys lineata*
  - *Helicops leopardinus*
    - *schistosus*
  - *Heterodon nasicus*
    - *platyrhinos*
    - *simus*
  - *Holarchus cyclurus*
  - *Holuropholis olivaceus*
  - *Hydrodynastes gigas*
  - *Leimadophis melanotus*
    - *reginae*
  - *Leptodeira annulata*
    - *maculata*
    - *septentrionalis*
  - *Limnophis bicolor*
  - *Liophis anomala*
    - *cobella*
    - *miliaris*
  - *Lygophis flavifrenatus*

  - *lineatus*
- *Macrcphisthodon rudis*
- *Malpolon moilensis*
- *Mimophis mahfalensis*
- *Natriciteres olivacea*
- *Natrix piscator*
  - *stolata*
  - *trianguligera*
- *Opheodrys aestivus*
  - *major*
  - *vernalis*
- *Opisthoplus degener*
- *Oxybelis aeneus*
  - *fulgidus*
- *Passerita mycterizans*
  - *nasuta*
  - *prasinus*
- *Philothalmus heterodermus*
  - *irregularis*
- *Psammodynastes pictus*
  - *pulverulentus*
- *Psammophis sibilans*
  - *subtaeniatus*
- *Pseudoxenodon sinensis*
  - *striaticaudatus*
- *Pseustes poecilonotus*
  - *sulphureus*
- *Ptyas korros*
  - *mucosus*
- *Rhadinaea seperaster*
- *Rhamnophis aethiopissa*
- *Rhynchocalamus melanocephalus*
- *Salvadora bairdi*
  - *grahami*
  - *hexalepis*
  - *lemniscata*
  - *lineata*
  - *mexicana*
- *Sibon sibon*
- *Sibynomorphus turgidus*
- *Simophis rhinostoma*
- *Spalerosophis diadema*
- *Stegonotus borneensis*
  - *magnus*
- *Stenorhina degenhardti*
- *Storeria dekayi*
  - *occipitomaculata*
- *Tachymenis chilensis*
- *Telescopus iberus*
  - *semiannulatus*
- *Thamophis butleri*
  - *eques*
  - *macrostemma*
  - *marcianus*
  - *radix*
  - *sauritus*
  - *sirtalis*
- *Thelotornis kirtlandii*
- *Thrasops flavigularis*
- *Tomodon dorsatus*
  - *ocellatus*
- *Trimorphodon lambda*
- *Trirhinopholis styani*
- *Tropidoclonium lineatum*
- *Trcpidodipsas fischeri*
- *Xenodon merremii*
  - *severus*
- *Zaocys dhumnades*
  - *nigromarginatus*

- Elapidae
  - *Acanthophis antarcticus*
  - *Aspidelaps scutatus*
  - *Boulengerina annulata*
  - *Brachyaspis curta*
  - *Brachyurophis semifasciata*
  - *Bungarus candidus*
    - *fasciatus*
    - *multicinctus*
  - *Demansia olivacea*
  - *Dendroaspis angusticeps*
    - *jamesoni*
    - *polylepis*
    - *viridis*
  - *Denisonia par*
    - *woodfordi*
  - *Elapscidea sundevalli*
  - *Hemachatus haemachatus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Micropechis elapsoides*
  - *Micruroides euryxanthus*
  - *Micrurus affinis*
    - *fulvius*
    - *mipartitus*
    - *nigrocinctus*
    - sp.
    - *spixi*
  - *Naja flava*
    - *haje*
    - *melanoleuca*

- *naja*
- *nigricollis*
- *nivea*
- *Ogmodon vitianus*
- *Ophiophagus hannah*
- *Pseudohaje goldii*
    - *nigra*
- *Walterinnesia aegyptia*

Hydrophiidae
- *Hydrelaps*
- *Hydrophis ornatus*
- *Laticauda colubrina*
    - *laticaudata*
- *Microcephalophis cantoris*
- *Thalassophina viperina*

Viperinae
- *Adenorhinos*
- *Atheris*
- *Bitis*
- *Cerastes*
- *Echis*
- *Eristicophis*
- *Vipera*

State II arose from State I because there is intraspecific variation in one taxon and intrageneric variation in others.

Character State III is rare in the colubrids (table 94) (Criterion 2). It occurs in the following colubrids (plus other taxa):

Colubridae
- *Aparallactus lunulatus*
- *Elapomorphus blumii*
- *Hydrops triangularis*
- *Lycodon striatus*
- *Lycophidion capense*
- *Mehelya capensis*
    - *chanleri*
    - *poensis*
- *Miodon gabonensis*
- *Pseudorhabdion collaris*
    - *longiceps*
- *Scaphiophis albopunctatus*

Elapidae
- *Aspidelaps lubricus*
- *Aspidomorphus lineaticollis*
- *Cacophis harriettae*
- *Demansia textilis*
- *Denisonia nigrescens*
    - *superba*
- *Elapognathus minor*
- *Elaps lacteus*
- *Furina diadema*
- *Hoplocephalus bungaroides*
- *Oxyuranus scutellatus*
- *Parapistocalamus hedigeri*
- *Pseudechis australis*
    - *papuanus*
- *Rhynchoelaps bertholdi*
- *Toxicocalamus stanleyanus*
- *Ultrocalamus preussi*
- *Vermicella annulata*

Hydrophiidae
- *Acalyptophis*
- *Aipysurus*
- *Astrotia*
- *Emydocephalus*
- *Enhydrina*
- *Ephalophis*
- *Hydrophis belcheri*
    - *brookii*
    - *caerulescens*
    - *cyanocinctus*
    - *fasciatus*
    - *inornatus*
    - *kingi*
    - *lapemis*
    - *major*
    - *mamillaris*
    - *melanocephalus*
    - *melanosoma*
    - *merteni*
    - *torquatus*
- *Kerilia*
- *Kolpophis*
- *Lapemis*
- *Microcephalophis gracilis*
- *Pelamis*
- *Thalassophis anomalus*

In these colubrids, Character State III has a higher frequency of correlation with derived states of 13 other characters compared to the frequency distribution of these states of the same 13 characters in the total sample (table 98) (Criterion 3).

Also these colubrids have a larger number of species confined to the fossorial habitat (41.7 per cent) compared to the abundance of fossorial colubrid species in the total sample (12.4 per cent) (table 97) (Criterion 5).

In addition these colubrids have a significantly larger number of species confined to tropical Africa (58.3 per cent) compared to the relative abundance of tropical African colubrids in the total sample (14.3 per cent) (table 96) (Criterion 6).

The application of four criteria (2–3, 5–6) strongly suggests that this state is derived (Criterion 8).

Character State IV is rare in the colubrids (table 94) (Criterion 2). It occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Enhydris chinensis*
    - *enhydris*
    - *plumbea*
  - *Holarchus formosanus*
    - *hainensis*
  - *Homalopsis buccata*
  - *Tantilla gracilis*
- Hydrophiidae
  - *Hydrophis klossi*
  - *Laticauda schistorhynchus*
    - *semifasciata*
- Elapidae
  - *Aspidomorphus muelleri*
  - *Calliophis japonicus*
  - *Hoplocephalus bitorquatus*
  - *Maticora bivirgata*
  - *Micropechis ikaheka*
  - *Pseudechis porphyrianus*
- Viperinae
  - *Causus*
- *Azemiops*
- *Atractaspis*

In these colubrids character State IV has a higher frequency of correlation with derived states of seven other characters compared to the frequency distribution of these states of the same seven characters in the total sample (table 98) (Criterion 3).

Also these colubrids have a larger number of species confined to the aquatic habitat (57.1 per cent) compared to the abundance of aquatic colubrid species in the total sample (14.9 per cent) (table 97) (Criterion 5).

In addition, these colubrids have a significantly larger number of species confined to eastern Asia (57.1 per cent) compared to the relative abundance of eastern Asian colubrids in the total sample (10.8 per cent) (table 96) (Criterion 6).

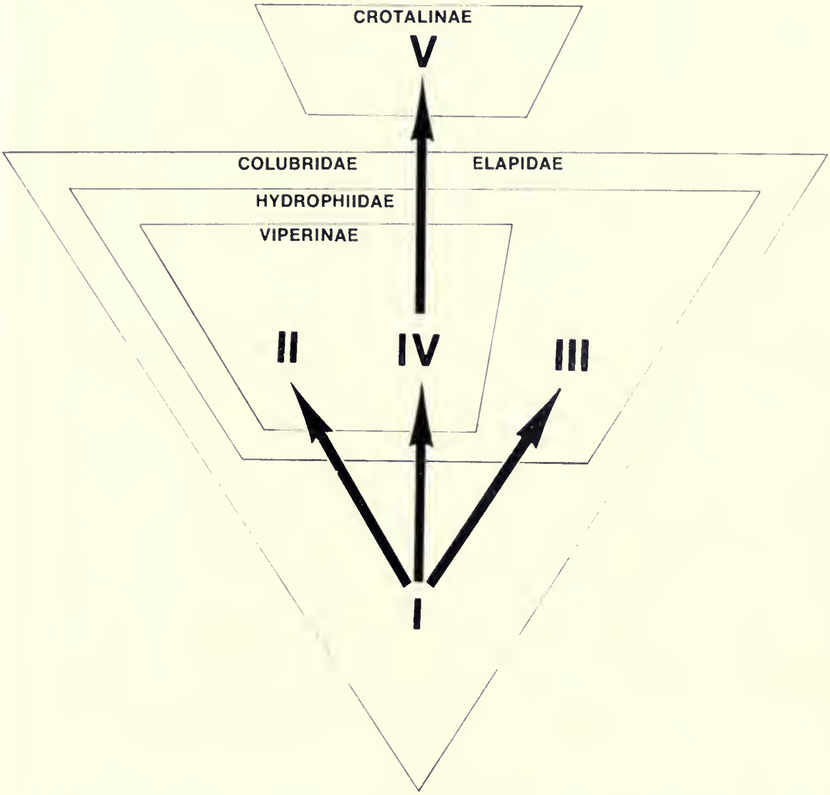

FIG. 32. Distribution among families of states of Character 33. Direction of change among states shown by arrows.

The application of four criteria (2, 3, 5, 6) strongly suggests that this state is derived (Criterion 8).

States II, III, and IV probably did not derive from each other. The colubrids with each of these states are predominantly abundant in different habitat zones (table 97) and different geographic areas (table 96) and where significant (III, IV) correlate mostly with derived states of different characters (table 98). Therefore, we suggest that all three derived states arose independently from the primitive State I.

State V occurs solely in the crotalines. The uniqueness criterion applies, and the state is thus derived. Its derivation was probably through a less mobile articular arrangement, and State IV seems the most likely such stage, occurring as it does in *Causus* and *Azemiops*, the relatively primitive taxa within the viperids. There may be a parallel in the occurrence of State IV in the primitive *Laticauda* and *Hydrophis* in the hydrophiids and its confinement to Indoaustralian taxa among the elapids. It is also of interest to find it in the "folding-fang" false viper *Atractaspis*.

TABLE 98. Correlation of States III and IV of Character 33 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State III of Character 33 | In species having State IV of Character 33 | In total working sample |
| 1 | | 57.1% (2) | 14.3% (28) |
| 7 | 50.0% (5)* | | 25.5 (56) |
| 9 | 25.0 (2) | | 6.8 (14) |
| 16 | | 42.9 (2) | 21.7 (34) |
| 19 | 75.0 (6) | 100.0 (3) | 36.8 (68) |
| 28 | 37.5 (3) | | 11.7 (26) |
| 29 | 60.0 (6) | | 10.1 (27) |
| 31 | | 57.1 (2) | 19.5 (44) |
| 32 | 44.4 (4) | 57.1 (3) | 26.3 (55) |
| 34 | 40.0 (3) | | 6.8 (18) |
| 36 | 50.0 (5) | | 6.1 (16) |
| 37 | 58.3 (6) | | 22.9 (54) |
| 39 | 42.9 (3) | 42.9 (2) | 9.0 (15) |
| 43 | 36.4 (2) | | 1.9 (3) |
| 46 | | 71.4 (3) | 26.9 (52) |
| 49 | 50.0 (2) | | 15.5 (26) |
| 50 | 42.9 (2) | | 20.0 (24) |

* Number of genera.

Our interpretation of the phyletics of Character 33 is shown in Figure 32.

## Character 34—Anterolateral Wing of Frontal

### DESCRIPTION OF CHARACTER

The frontal bone articulates with the prefrontal in several places. On the frontal there is often an anterolateral projection extending before the anteromedial face of the prefrontal. This bony projection can best be viewed from a frontal position.

Two states are recognized:

State I —wing absent
State II —wing present

TABLE 99. Distribution of character states of the antero-lateral wing of the frontal.

| Description | STATES<br>II<br>Present | <br>I<br>Absent | INTRAGENERIC VARIATION |
|---|---|---|---|
| | SPECIES[1] | | |
| Colubridae —295 | 93.2% | 6.8% | |
| Elapidae — 43 | 93.0 | 7.0 | |
| Hydrophiidae — 35 | 97.1 | 2.9 | |
| Viperinae — 34 | 100.0 | | |
| Crotalinae — 45 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 4 | | 100.0 | |
| | GENERA | | |
| Colubridae —157 | 88.5 | 9.6 | 1.9% |
| Elapidae — 27 | 92.6 | 7.4 | |
| Hydrophiidae — 14 | 92.9 | 7.1 | |
| Viperinae — 8 | 100.0 | | |
| Crotalinae — 6 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | | 100.0 | |

[1] Working sample.

## FAMILIAL RANGES OF VARIATION (Table 99)

Colubridae—This family has both states in a sample of 295 species of 157 genera (553 skulls). State I occurs in 20 species of 18 genera (49 skulls), II in 275 species of 142 genera (504 skulls). Intrageneric variation occurs in 3 genera (*Atractus, Lytorhynchus, Mehelya*).

Elapidae—This family has both states in a sample of 43 species of 27 genera (81 skulls). State I occurs in 3 species of 2 genera (5 skulls), II in 40 species of 25 genera (76 skulls).

Hydrophiidae—The sea snakes have both states in a sample of 35 species of 14 genera (129 skulls). State I occurs in monotypic *Acalyptophis* (1 skull), II in 34 species of 13 genera (128 skulls).

Viperinae—The true vipers have State II in a sample of 34 species of the 8 genera (95 skulls).

Crotalinae—The pit vipers have State II in a sample of 45 species of the 6 genera (82 skulls).

*Azemiops* has State II (2 skulls).

*Atractaspis* has State I in a sample of 4 species (7 skulls).

TABLE 100. Correlation of State I of Character 34 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State I of Character 34 | In total working sample |
| 1 | 25.0% (5)* | 14.3% (28) |
| 5 | 15.0 (3) | 3.5 (9) |
| 7 | 60.0 (11) | 25.5 (56) |
| 19 | 84.2 (14) | 36.8 (68) |
| 22 | 20.0 (4) | 4.5 (11) |
| 28 | 35.3 (6) | 11.7 (26) |
| 29 | 38.9 (7) | 10.1 (27) |
| 31 | 41.2 (7) | 19.5 (44) |
| 32 | 61.1 (10) | 26.3 (55) |
| 35 | 15.8 (3) | 2.0 (6) |
| 36 | 22.2 (4) | 6.1 (16) |
| 37 | 40.0 (8) | 22.9 (54) |
| 38 | 58.3 (7) | 16.2 (27) |
| 39 | 33.3 (4) | 9.0 (15) |
| 40 | 35.0 (7) | 24.8 (54) |
| 41 | 25.0 (3) | 10.9 (20) |
| 42 | 38.5 (5) | 8.7 (14) |
| 43 | 15.8 (3) | 1.9 (3) |
| 44 | 36.4 (4) | 5.8 (11) |
| 49 | 61.5 (7) | 15.5 (26) |
| 50 | 53.8 (5) | 20.0 (24) |

* Number of genera.

## PHYLETICS OF CHARACTER 34

Character State I is rare in the colubrids (table 99) (Criterion 2).

State I, absence of the anterolateral wing of the frontal, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Amastridium veliferum*
  - *Aparallactus werneri*
  - *Aspidura trachyprocta*
  - *Atractus erythromelas*
    - *latifrons*
  - *Boaedon lineatus*
  - *Calamaria septentrionalis*
  - *Calamelaps unicolor*
  - *Carphophis amoena*
  - *Chilorhinophis carpenteri*
  - *Cyclocorus lineatus*
  - *Lycophidion capense*
  - *Lytorhynchus diadema*
  - *Mehelya chanleri*
    - *poensis*
  - *Miodon gabonensis*
  - *Prosymna ambigua*
  - *Sibon sibon*
  - *Sibynomorphus turgidus*
  - *Tantilla gracilis*
- Elapidae
  - *Demansia olivacea*
    - *textilus*
  - *Leptomicrurus narducci*
- Hydrophiidae
  - *Acalyptophis peronii*
- *Atractaspis*

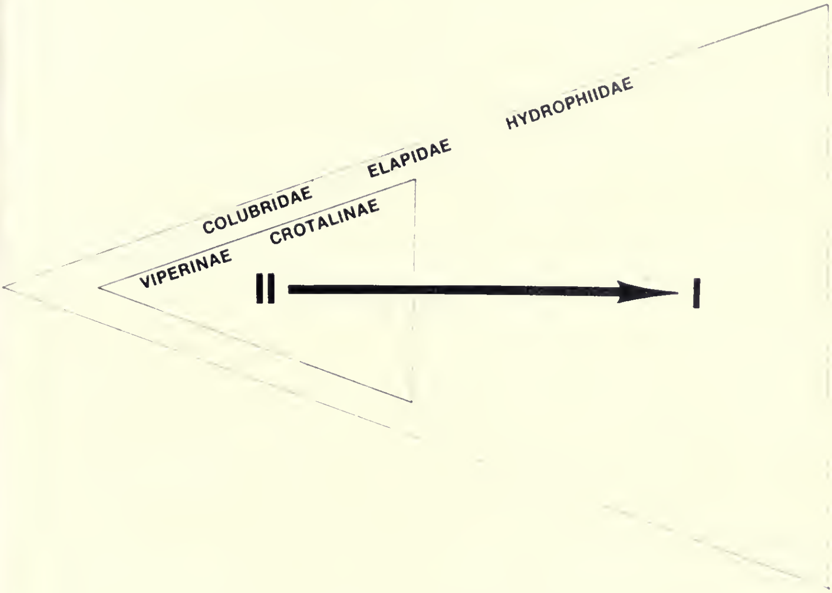

FIG. 33. Distribution among families of states of Character 34. Direction of change among states shown by arrows.

In these colubrids this character state has a higher frequency of correlation with derived states of 21 other characters compared to the frequency distribution of these states of the same 21 characters in the total sample (table 100) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—75.0 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent—table 101) (Criterion 5).

TABLE 101. Habitat distribution of colubrid species having State I of Character 34 compared to the total colubrid working sample.

| | Total working Sample | State I Character 34 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 15.0 |
| Arboreal | 16.5 | 10.0 |
| Aquatic | 14.9 | |
| Subterrestrial | 10.8 | 30.0 |
| Fossorial | 12.4 | 45.0 |
| Variation | 5.3 | |
| Unknown | 3.5 | |

The application of three criteria (2, 3, 5) suggests that State I is derived (Criterion 8).

Our interpretation of the phyletics of Character 34 is shown in Figure 33.

## Character 35—Postorbital Bone

### DESCRIPTION OF CHARACTER

The postorbital bone (postfrontal of Albright and Nelson, 1959, p. 198) lies posterior to the orbit (Peters, 1964, p. 275).

Two states are recognized:

State I —postorbital present
State II —postorbital absent

### FAMILIAL RANGES OF VARIATION (Table 102)

Colubridae—This family has both states in a sample of 307 species of 163 genera (565 skulls). State I occurs in 301 species of 158 genera (557 skulls), II in 6 species of 6 genera (8 skulls).

Intrageneric variation occurs in *Geophis*, as also observed by Downs (1967, p. 24).

TABLE 102. Distribution of character states of the postorbital.

| | STATES | | |
|---|---|---|---|
| | I | II | |
| Description | Present | Absent | |
| | SPECIES[1] | | |
| Colubridae —307 | 98.0% | 2.0% | |
| Elapidae — 66 | 78.8 | 21.2 | |
| Hydrophiidae— 42 | 100.0 | | |
| Viperinae — 34 | 100.0 | | |
| Crotalinae — 44 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 5 | | 100.0 | |
| | GENERA | | INTRAGENERIC VARIATION |
| Colubridae —163 | 96.3 | 3.1 | 0.6% |
| Elapidae — 36 | 80.6 | 19.4 | |
| Hydrophiidae— 16 | 100.0 | | |
| Viperinae — 8 | 100.0 | | |
| Crotalinae — 6 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | | 100.0 | |

[1] Working sample.

Elapidae—This family has both states in a sample of 66 species of 36 genera (108 skulls). State I occurs in 52 species of 29 genera (90 skulls), II in 14 species of 7 genera (18 skulls).

Hydrophiidae, Viperinae, Crotalinae—The sea snakes, true vipers, and pit vipers all have State I in a sample of 120 species (42, 34, 44 respectively) of 30 genera (16, 8, 6) (319 skulls: 143, 95, 81 skulls).

*Azemiops* has State I (2 skulls).

*Atractaspis* has State II in a sample of 5 species (8 skulls).

### Phyletics of Character 35

Character State II is rare in the colubrids (table 102) (Criterion 2).

State II, postorbital absent, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Dryocalamus davisoni*
  - *Geophis semidoliatus*
  - *Miodon gabonensis*
  - *Oxyrhabdium modestum*
- Elapidae
  - *Calliophis japonicus*
  - *Elaps lacteus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Micruroides euryxanthus*
  - *Micrurus affinis*
    - *fulvius*
    - *lemniscatus*
    - *mipartitus*
    - *nigrocinctus*
    - sp.
    - *spixi*
  - *Toxicocalamus stanleyanus*
  - *Ultrocalamus preussi*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of 15 other characters compared to the frequency distribution of these states of the same 15 characters in the total sample (table 103) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the fossorial habitat (83.3 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

The presence of this character state in three African colubrid genera representative of the Aparallactinae group probably reflects a homologous condition in these snakes. Its occurrence in *Atrac-*

TABLE 103. Correlation of State II of Character 35 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State II of Character 35 | In total working sample |
| 7 | 83.5% (6)* | 25.5% (56) |
| 13 | 50.0 (3) | 31.8 (54) |
| 19 | 66.7 (4) | 36.8 (68) |
| 29 | 100.0 (5) | 10.1 (27) |
| 31 | 50.0 (6) | 19.5 (44) |
| 32 | 66.7 (4) | 26.3 (55) |
| 34 | 50.0 (3) | 6.8 (18) |
| 36 | 66.7 (4) | 6.1 (16) |
| 38 | 80.0 (5) | 16.2 (27) |
| 40 | 60.0 (5) | 24.8 (54) |
| 42 | 60.0 (5) | 8.7 (14) |
| 44 | 60.0 (5) | 5.8 (11) |
| 46 | 50.0 (3) | 26.9 (52) |
| 49 | 60.0 (5) | 15.5 (26) |
| 50 | 80.0 (5) | 20.0 (24) |

* Number of genera.

*taspis* probably reflects a close relationship of this genus with the Aparallactines. This pattern is repeated in other characters. Though these species are all burrowers, this character state does not occur in many other burrowers so that this adaptive feature is restricted to a monophyletic stock in one geographic area. Also burrowing elapids may or may not have State II. All of the New World elapids having State II are secretive coral snakes, whereas only two of 10 Australian elapid burrowers have this state. In other words, there are many ways to burrow, but within groups the morphological pattern is narrowly determined.

Our interpretation of the phyletics of Character 35 is shown in Figure 34.

## Character 36—Anterolateral Process of Parietal

### Description of Character

In most colubroid snakes the parietal and frontal unite dorsally along a straight suture perpendicular to the long axis of the skull. In some taxa, however, the parietal extends forward laterally to border the frontal on its side. This anterolateral process may or may not form part of the dorsal margin of the orbit.

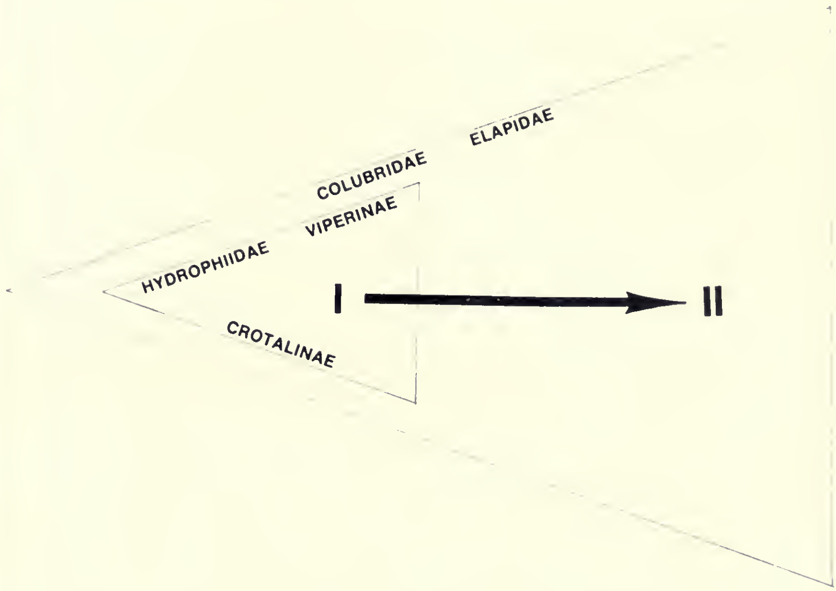

FIG. 34. Distribution among families of states of Character 35. Direction of change among states shown by arrows.

Three states are recognized:

State I —process absent
State II —process present, forms orbital edge
State III—process present, does not form orbital edge

### FAMILIAL RANGES OF VARIATION (Table 104)

Colubridae—This family has all three states in a sample of 310 species of 162 genera (569 skulls). State I occurs in 291 species of 148 genera (537 skulls), II in 8 species of 7 genera (13 skulls), III in 11 species of 10 genera (19 skulls).

Intrageneric variation occurs in three genera: *Atractus* has States I and II; *Liophis* has States I and III; *Geophis* has States II and III.

Elapidae—This family has all three states in a sample of 68 species of 37 genera (110 skulls). State I occurs in 41 species of 22 genera (76 skulls), II in 17 species of 10 genera (22 skulls), III in 10 species of 7 genera (12 skulls).

Intrageneric variation occurs in two genera: *Aspidomorphus* and *Bungarus* have States I and III.

TABLE 104. Distribution of character states of the antero-lateral process of the parietals.

| | STATES | | | | | |
|---|---|---|---|---|---|---|
| | I | II | III | | | |
| Description | Absent | Forms Orbital Edge | Does not Form Orbital Edge | | | |
| | SPECIES[1] | | | | | |
| Colubridae —310 | 93.9% | 2.6% | 3.5% | | | |
| Elapidae — 68 | 60.3 | 25.0 | 14.7 | | | |
| Hydrophiidae— 42 | 28.6 | 4.8 | 66.7 | | | |
| Viperinae — 34 | 100.0 | | | | | |
| Crotalinae — 45 | 100.0 | | | | | |
| *Azemiops* — 1 | 100.0 | | | | | |
| *Atractaspis* — 5 | 100.0 | | | | | |
| | GENERA | | | INTRAGENERIC VARIATION | | |
| | | | | I, II | I, III | II, III |
| Colubridae —162 | 90.1 | 3.1 | 4.9 | 0.6% | 0.6% | 0.6% |
| Elapidae — 37 | 54.1 | 27.0 | 13.5 | 2.7 | 5.4 | |
| Hydrophiidae— 16 | 25.0 | 6.3 | 56.3 | | 12.5 | |
| Viperinae — 8 | 100.0 | | | | | |
| Crotalinae — 6 | 100.0 | | | | | |
| *Azemiops* — 1 | 100.0 | | | | | |
| *Atractaspis* — 1 | 100.0 | | | | | |

[1] Working sample.

Hydrophiidae—The sea snakes have all three states in a sample of 42 species of the 16 genera (143 skulls). State I occurs in 12 species of 6 genera (34 skulls), II in 2 species of *Microcephalophis* (2 skulls), III in 28 species of 11 genera (107 skulls).

Intrageneric variation occurs in two genera: *Laticauda* and *Hydrophis* have States I and III.

Viperinae, Crotalinae, *Azemiops, Atractaspis*—These four taxa all have State I in a sample of 85 species (34, 45, 1, 5 respectively) of the 16 genera (8, 6, 1, 1) (187 skulls: 95, 82, 2, 8).

## PHYLETICS OF CHARACTER 36

Character State II is rare in the colubrids (table 104) (Criterion 2).

State II, anterolateral process of the parietals forming the orbital edge, occurs in the following colubrids (plus other taxa):

Colubridae
  *Achalinus spinalis*
*Atractus ventrimaculatus*
*Brachyorrhus albus*

*Chilorhinophis carpenteri*
*Geophis semidoliatus*
*Lycodon aulicus*
  *striatus*
*Miodon gabonensis*
Elapidae
  *Brachyurophis semifasciata*
  *Calliophis japonicus*
  *Elaps lacteus*
  *Leptomicrurus collaris*
    *narducci*
  *Micruroides euryxanthus*
  *Micrurus affinis*
    *fulvius*
    *lemniscatus*
    *mipartitus*
    *nigrocinctus*
    sp.
    *spixi*
  *Rhynchoelaps bertholdi*
  *Toxicocalamus stanleyanus*
  *Ultrocalamus preussi*
  *Vermicella annulata*
Hydrophiidae
  *Microcephalophis*

In these colubrids this character state has a higher frequency of correlation with derived states of 13 other characters compared to the frequency distribution of these states of the same 13 characters in the total sample (table 105) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the fossorial habitat (62.5 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (table 106) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

Character State III is rare in the colubrids (table 104) (Criterion 2).

State III, anterolateral process of the parietals not forming the orbital edge, occurs in the following colubrids (plus other taxa):

Colubridae
  *Aparallactus lunulatus*
  *Aspidura trachyprocta*
  *Elapomorphus blumii*
  *Geophis multitorques*
  *Haldea striatula*
    *valeriae*
  *Hydrops triangularis*
  *Liophis anomala*
  *Lycophidion capense*
  *Oxyrhabdium modestum*
  *Tropidocloniom lineatum*
Elapidae
  *Aspidomorphus muelleri*
  *Bungarus multicinctus*
  *Cacophis harriettae*
  *Furina diadema*
  *Maticora bivirgata*
  *Micropechis elapsoides*
    *ikaheka*
  *Pseudechis australis*
    *papuanus*
    *porphyriacus*
Hydrophiidae
  *Acalyptophis*
  *Astrotia*
  *Enhydrina*
  *Hydrelaps*

*Hydrophis belcheri*
*brookii*
*caerulescens*
*cyanocinctus*
*fasciatus*
*inornata*
*kingi*
*klossi*
*lapemoides*
*major*
*mamillaris*
*melanocephalus*
*melanosoma*
*ornatus*
*torquatus*
*Kerilia*
*Kolpophis*
*Lapemis*
*Laticauda colubrina*
*laticaudata*
*schistorhynchus*
*Thalassophina*
*Thalassophis*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 105) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—81.8 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent—table 106) (Criterion 5).

TABLE 105. Correlation of States II and III of Character 36 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 36 | In species having State III of Character 36 | In total working sample |
| 7 | 75.0% (6)* | 63.6% (7) | 25.5% (56) |
| 13 | 62.5 (5) | | 31.8 (54) |
| 19 | 75.0 (6) | 81.8 (8) | 36.8 (68) |
| 22 | 37.5 (3) | | 4.5 (11) |
| 27 | 50.0 (2) | | 17.9 (40) |
| 28 | | 55.6 (5) | 11.7 (26) |
| 29 | 42.9 (3) | 33.3 (3) | 10.1 (27) |
| 32 | 50.0 (4) | 57.1 (4) | 26.3 (55) |
| 33 | | 81.8 (8) | 43.0 (76) |
| 35 | 50.0 (3) | | 2.0 (6) |
| 37 | 75.0 (5) | | 22.9 (54) |
| 38 | 62.5 (5) | | 16.2 (27) |
| 40 | 75.0 (5) | | 24.8 (54) |
| 42 | 42.9 (3) | | 8.7 (14) |
| 50 | 42.9 (3) | | 20.0 (24) |

* Number of genera.

TABLE 106. Habitat distribution of colubrid species having States II and III of Character 36 compared to the total colubrid working sample.

| | Total Working Sample | State II Character 36 | State III Character 36 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | 25.0 | 9.1 |
| Arboreal | 16.5 | | |
| Aquatic | 14.9 | | 9.1 |
| Subterrestrial | 10.8 | 12.5 | 54.5 |
| Fossorial | 12.4 | 62.5 | 27.3 |
| Variation | 5.3 | | |
| Unknown | 3.5 | | |

The application of these criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

With so few colubrid taxa in the two derived states, the phyletic question is a tenuous proposition. A first question is whether we are not dealing with two separate characteristics, for State II by definition includes a State III condition. That the two states are directly linked is suggested by the intrageneric variation in *Geophis* and also

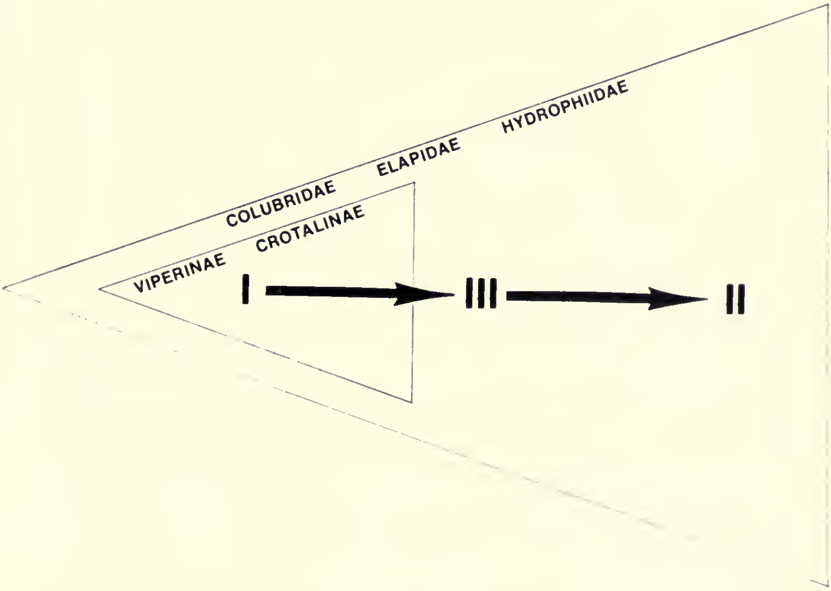

FIG. 35. Distribution among families of states of Character 36. Direction of change among states shown by arrows.

by the general correlations of these states with progressively more specialized morphological and ecological conditions. In respect to this, State II appears as the more derivative, as suggested by its more numerous correlates among derived states of other characters (13 *versus* 6 for State III). In addition, State II occurs in a higher proportion of fossorial colubrid taxa, whereas State III is more characteristic of a subterrestrial mode of life.

When the elapids and hydrophiids are considered, State II appears rather directly associated with modifications resulting in a small, elongate head.

Our interpretation of the phyletics of Character 36 is shown in Figure 35.

## Character 37—Parietal Bone

### Description of Character

The parietal bone usually has its lateral surface bowed outward, giving the posterior braincase a bulbous shape. The bulbous area may involve most of the lateral surface or be localized. The localization is usually associated with an elongated posterior section of the skull. We recognize the following conditions:

State I —non-bulbous
State II —moderately bulbous overall
State III—parietal bulbous anteriorly
State IV—parietal bulbous medially

### Familial Ranges of Variation (Table 107)

Colubridae—This family has all four states in a sample of 314 species of 166 genera (573 skulls). State I occurs in 38 species of 27 genera (89 skulls), II in 243 species of 126 genera (430 skulls), III in 25 species of 21 genera (43 skulls), IV in 8 species of 6 genera (11 skulls).

Intrageneric variation occurs in 15 genera: *Arrhyton, Atractus, Geophis* (II, III); *Enhydris* (II, IV); *Clelia, Coluber, Drymobius, Elaphe, Malpolon, Masticophis, Natrix, Passerita, Pseudoboa, Thamnophis* (II, I); *Boiga* (II, III, I).

Elapidae—This family has all four states in a sample of 69 species of 38 genera (111 skulls). State I occurs in 3 species of 3 genera (8

TABLE 107. Distribution of character states of the bulbous expansion of the parietal bone.

| | STATES | | | | INTRAGENERIC VARIATION | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | I | II | III | IV | II, III | II, IV | II, I | II, III, IV | II, III, I |
| Description | Non-bulbous | Bulbous moderately | Bulbous anteriorly | Bulbous medially | | | | | |
| | | SPECIES | | | | | | | |
| Colubridae —314 | 12.1% | 77.4% | 8.0% | 2.5% | | | | | |
| Elapidae — 69 | 4.3 | 42.0 | 2.9 | 50.7 | | | | | |
| Hydrophiidae— 42 | 4.8 | 45.2 | 16.7 | 33.3 | | | | | |
| Viperinae — 34 | | 76.5 | 23.5 | | | | | | |
| Crotalinae — 45 | 6.7 | 88.9 | 4.4 | | | | | | |
| *Azemiops* — 1 | | | 100.0 | | | | | | |
| *Atractaspis* — 5 | | | 100.0 | | | | | | |
| | | GENERA | | | | | | | |
| Colubridae —166 | 10.2 | 67.5 | 10.2 | 3.0 | 1.8% | 0.6% | 6.0% | | 0.6% |
| Elapidae — 38 | 7.9 | 34.2 | 5.3 | 44.7 | | 17.9 | | | |
| Hydrophiidae— 16 | 6.3 | 31.3 | | 37.5 | 6.3 | | 6.3 | 12.5% | |
| Viperinae — 8 | | 50.0 | 25.0 | | 25.0 | | | | |
| Crotalinae — 6 | 16.7 | 50.0 | | | 16.7 | | | | 16.7 |
| *Azemiops* — 1 | | | 100.0 | | | | | | |
| *Atractaspis* — 1 | | | 100.0 | | | | | | |

skulls), II in 29 species of 16 genera (56 skulls), III in 2 species of 2 genera (3 skulls), IV in 35 species of 20 genera (44 skulls).

Intrageneric variation occurs in three genera: *Aspidomorphus, Denisonia, Pseudechis* (II, IV).

Hydrophiidae—The sea snakes have all four states in a sample of 42 species of the 16 genera (143 skulls). State I occurs in 2 species of 2 genera (4 skulls), II in 19 species of 9 genera (72 skulls), III in 7 species of 3 genera (19 skulls), IV in 14 species of 8 genera (48 skulls).

Intrageneric variation occurs in 4 genera: *Emydocephalus* (II, III); *Aipysurus* (II, I); *Hydrophis, Laticauda* (II, III, IV).

Viperinae—The true vipers have States II and III in a sample of 34 species of the 8 genera (95 skulls). State II occurs in 26 species of 6 genera (78 skulls), III in 8 species of 4 genera (17 skulls).

Intrageneric variation occurs in two genera: *Bitis, Echis.*

Crotalinae—The pit vipers have States I, II, and III in a sample of 45 species of the 6 genera (82 skulls). State I occurs in 3 species of 2 genera (6 skulls), II in 40 species of 5 genera (74 skulls), III in 2 species of 2 genera (2 skulls).

Intrageneric variation occurs in 2 genera: *Trimeresurus* (II, III) and *Agkistrodon* (II, III, I).

*Azemiops* has State III (2 skulls).

*Atractaspis* has State III in a sample of 5 species (8 skulls).

### PHYLETICS OF CHARACTER 37

Character State I is moderately rare in the colubrids (table 107). It occurs in the following colubrids (plus other taxa):

Colubridae
- *Abastor erythrogrammus*
- *Arizona elegans*
- *Boaedon lineatus*
- *Boiga dendrophila*
- *Bothrophthalmus lineatus*
- *Chironius carinatus*
  - *fuscus*
- *Chrysopelea ornata*
- *Clelia clelia*
- *Coluber constrictor*
- *Cyclagras gigas*
- *Dimades plicatilis*
- *Drymarchon corais*
- *Drymobius bifossatus*
- *Elaphe carinata*
- *Farancia abacura*
- *Hydrodynastes gigas*
- *Hydrops triangularis*
- *Leptophis mexicanus*
  - *occidentalis*
- *Macropisthodon rudis*
- *Malpolon monspessulanus*
- *Masticophis flagellum*
- *Natrix aequifasciata*
  - *cyclopion*
  - *erythrogaster*
  - *percarinata*
  - *rhombifera*

*sipedon*
*taxispilota*
*Passerita mycterizans*
*Pseudaspis cana*
*Pseudoboa claelia*
*Thamnophis marcianus*
*sirtalis*
*Xenodon colubrinus*
*merremii*
*severus*

Elapidae
*Acanthophis antarcticus*
*Hemachatus haemachatus*
*Ophiophagus hannah*
Hydrophiidae
*Aipysurus laevis*
*Astrotia stokesii*
Crotalinae
*Agkistrodon acutus*
*bilineatus*
*Lachesis mutus*

In these colubrids this character state has a higher frequency of correlation with derived states of five other characters compared to the frequency distribution of these states of the same five characters in the total sample (table 108) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the aquatic habitat (31.6 per cent) compared to the relative abundance of aquatic colubrid species in the total sample (14.9 per cent—table 109) (Criterion 5).

These colubrids are also predominantly from the New World (81.6 per cent) (Criterion 6).

TABLE 108. Correlation of States I, III, and IV of Character 37 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State I of Character 37 | In species having State III of Character 37 | In species having State IV of Character 37 | In total working sample |
| 7 | | | 62.5% (4) | 25.5% (56) |
| 13 | | | 50.0 (4) | 31.8 (54) |
| 16 | 36.8% (9)* | | | 21.7 (34) |
| 19 | | 72.0% (14) | 75.0 (5) | 36.8 (68) |
| 22 | | | 37.5 (3) | 4.5 (11) |
| 27 | | | 66.7 (3) | 17.9 (40) |
| 28 | | 28.6 (5) | | 11.7 (26) |
| 29 | | | 57.1 (4) | 10.1 (27) |
| 32 | | 54.2 (10) | 66.7 (4) | 26.3 (55) |
| 33 | | | 75.0 (5) | 43.0 (76) |
| 34 | | 25.0 (6) | | 6.8 (18) |
| 36 | | 16.7 (4) | 62.5 (4) | 6.1 (16) |
| 38 | 26.5 (5) | | 60.0 (3) | 16.2 (27) |
| 39 | 23.5 (6) | | | 9.0 (15) |
| 40 | | | 60.0 (2) | 24.8 (54) |
| 48 | 35.7 (5) | | | 6.2 (11) |
| 49 | 42.9 (5) | | | 15.5 (26) |

* Number of genera.

TABLE 109. Habitat distribution of colubrid species having States I, III, and IV of Character 37 compared to the total colubrid sample.

| | Total working sample | Character 37 | | |
|---|---|---|---|---|
| | | State I | State III | State IV |
| Terrestrial | 36.2% | 42.1% | 16.0% | 25.0% |
| Arboreal | 16.5 | 7.9 | 16.0 | |
| Aquatic | 14.9 | 31.6 | 4.0 | 12.5 |
| Subterrestrial | 10.8 | 5.3 | 24.0 | 12.5 |
| Fossorial | 12.4 | 2.6 | 32.0 | 50.0 |
| Variation | 5.3 | 7.9 | | |
| Unknown | 3.5 | 2.6 | 8.0 | |

The application of four criteria (2, 3, 5, 6) suggests that this state is derived (Criterion 8).

We wish to note that only two genera of subterrestrial snakes have this state. They are *Abastor* and *Farancia,* which we strongly suspect will prove to be congeneric upon future investigation. Note, too, that these are perhaps more properly classed as subterrestrial-aquatic.

Character State III is rare in the colubrids (table 107) (Criterion 2).

State III, parietals bulbous anteriorly, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Achalinus spinalis*
  - *Amastridium veliferum*
  - *Arrhyton vittatum*
  - *Atractus elaps*
    - *erythromelas*
    - *ventrimaculatus*
  - *Boiga pulverulentus*
  - *Cryophis hallbergi*
  - *Darlingtonia haetiana*
  - *Drepanoides eatonii*
  - *Dugandia bicolor*
  - *Ficimia publia*
  - *Gastropyxis smaragdina*
  - *Geophis multitorques*
  - *Hypsiglena torquata*
  - *Lycophidion capense*
  - *Lytorhynchus diadema*
    - *maynardi*
  - *Phyllorhynchus decurtatus*
  - *Prosymna ambigua*
  - *Rhamnophis aethiopissa*
  - *Rhamphiophis oxyrhynchus*
  - *Sibynomorphus turgidus*
  - *Stegonotus borneensis*
    - *magnus*
- Elapidae
  - *Brachyurophis semifasciata*
  - *Parapistocalamus hedigeri*
- Hydrophiidae
  - *Emydocephalus annulatus*
  - *Hydrophis brooki*
    - *mamillaris*
    - *melanocephalus*
    - *mertoni*
    - *torquatus*
  - *Laticauda schistorhynchus*
- Viperinae
  - *Adenorhinos*
  - *Bitis heraldica*
  - *Causus*
  - *Echis coloratus*
- Crotalinae
  - *Agkistrodon strauchi*
  - *Trimeresurus puniceus*
- *Azemiops*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of five other characters compared to the frequency distribution of these states of the same five characters in the total sample (table 108) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the secretive habitats (subterrestrial and fossorial—56.0 per cent) compared to the relative abundance of secretive colubrid species in the total sample (23.2 per cent) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

Character State IV is very rare in the colubrids (table 107) (Criterion 2).

State IV, parietals bulbous medially, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Brachyorrhus albus*
  - *Elapomorphus blumii*
  - *Enhydris bocourti*
  - *Lycodon aulicus*
    - *striatus*
  - *Miodon gabonensis*
  - *Pseudorhabdion collaris*
    - *longiceps*
- Elapidae
  - *Apistocalamus lonnbergi*
    - *loriae*
  - *Aspidomorphus lineaticollis*
  - *Brachyaspis curta*
  - *Bungarus candidus*
    - *fasciatus*
    - *multicinctus*
  - *Cacophis harriettae*
  - *Calliophis japonicus*
  - *Denisonia coronoides*
    - *nigrescens*
    - *par*
    - *woodfordi*
  - *Elaps lacteus*
  - *Elapsoidea sundevalli*
  - *Furina diadema*
  - *Glyphodon tristis*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Micropechis elapsoides*
    - *ikaheka*
  - *Micruroides euryxanthus*
  - *Micrurus affinis*
    - *fulvius*
    - *lemniscatus*
    - *mipartitus*
    - *nigrocinctus*
    - sp.
    - *spixi*
  - *Pseudechis australis*
    - *papuanus*
  - *Rhynchoelaps bertholdi*
  - *Toxicocalamus stanleyanus*
  - *Ultrocalamus preussi*
  - *Vermicella annulata*
- Hydrophiidae
  - *Acalyptophis*
  - *Enhydrina*
  - *Ephalophis*
  - *Hydrelaps*
  - *Hydrophis belcheri*
    - *cyanocinctus*
    - *kingi*
    - *klossi*
    - *lapemoides*
    - *major*
  - *Laticauda colubrina*
  - *Microcephalophis*
  - *Thalassophis*

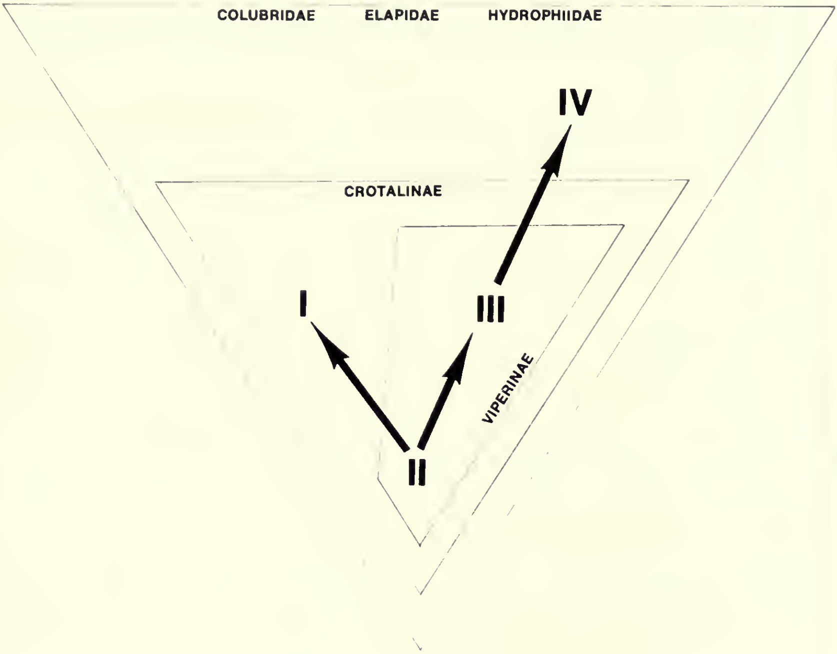

FIG. 36. Distribution among families of states of Character 37. Direction of change among states shown by arrows.

In these colubrids this character state has a higher frequency of correlation with derived states of 11 other characters compared to the frequency distribution of these states of the same 11 characters in the total sample (table 108) (Criterion 3).

These colubrids also have a markedly larger number of species confined to the fossorial habitat (50.0 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (Criterion 5).

Also seven of these eight colubrids are from the Old World (Criterion 6).

The application of four criteria (2, 3, 5, 6) suggests that this state is derived (Criterion 8).

State I probably is not derived from States III and IV. The colubrids with State I are predominantly abundant in different habitat zones (table 109) and correlate with mostly different derived character states than States III and IV (table 108). This different derivation is also indicated by the almost total lack of intrageneric variation of State I with the other derived states of Character 37 (table 107). Therefore, we suggest that State I stems directly from the primitive State II.

The taxa of States III and IV occur in the same habitat zones (table 109). However, State IV shows a greater number of derived state character correlates (11 *versus* 5) and in none of the three common character correlates is it less frequent than State III. Further, State IV taxa are more restricted ecologically, with a higher percentage of fossorial types. The association of State IV with burrowing extremes in the colubrids is supported by its predominance among the secretive elapids and contrasting total lack among the viperids. In the hydrophiids, which have a substantial percentage of taxa in both states, direct linkage of the states is suggested by intrageneric variation. We therefore propose that these states represent a single trend, and the more derivative state is IV.

Our interpretation of the phyletics of Character 37 is shown in Figure 36.

## Character 38—Relative Length of Quadrate

### Description of Character

The relative length of the quadrate is here defined as the length of the quadrate as a proportion of the total length of the skull. The maximum length of the quadrate is measured along its anterior edge (or lateral edge, depending upon its position on skull).

### Classes and States

The total range of variation in relative length of the quadrate was segmented by steps of 8.0 per cent, since a span of 8.0 per cent covered most of the intraspecific variation encountered (80.5 per cent—table 110). Nine classes resulted as shown in Table 111. The mean of each taxon was assigned to a class (table 111). States are established when there is a marked change in frequency of number of species between classes.

Three states are recognized:

State I —Classes 2–5 (21.0–52.9 per cent)
State II —Classes 6–9 (53.0–84.9)
State III—Class 1 (13.0–20.9)

TABLE 110. Spans in relative length of quadrate by species and families.

| Span | All families | Number of Species | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 227 | 146 | 22 | 16 | 17 | 26 |
| 2 | 1 | 1 | | | | |
| 3 | 1 | 1 | | | | |
| 4 | 2 | 2 | | | | |
| 6 | 3 | 1 | 1 | | | 1 |
| 7 | 6 | 5 | | | 1 | |
| 8 | 1 | 1 | | | | |
| 10 | 1 | | | | | 1 |
| 12 | 3 | 2 | 1 | | | |
| 13 | 1 | | | | 1 | |
| 14 | 2 | 1 | | | | 1 |
| 16 | 1 | 1 | | | | |
| 18 | 3 | 3 | | | | |
| 19 | 1 | 1 | | | | |
| 21–30 | 14 | 9 | 1 | 1 | 2 | 1 |
| 31–40 | 12 | 7 | 1 | 2 | 1 | 1 |
| 41–50 | 15 | 10 | 2 | 1 | 1 | 1 |
| 51–60 | 6 | 4 | 1 | 1 | | |
| 61–70 | 6 | 3 | | 1 | | 2 |
| 71–80 | 5 | 4 | | | | 1 |
| 81–90 | 8 | 3 | | 3 | 2 | |
| 91–100 | 7 | 5 | | 1 | 1 | |

TABLE 110. Spans in relative length of quadrate by species and families (*continued*).

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 101–110 | 2 | 2 |  |  |  |  |
| 111–120 | 6 | 2 | 1 |  | 1 | 2 |
| 121–130 | 3 | 2 |  |  |  | 1 |
| 131–140 | 2 | 1 |  | 1 |  |  |
| 141–150 | 3 |  |  |  | 3 |  |
| 151 | 1 |  |  | 1 |  |  |
| 164 | 2 | 1 | 1 |  |  |  |
| 166 | 1 |  |  |  | 1 |  |
| 171 | 1 | 1 |  |  |  |  |
| 184 | 1 |  |  |  | 1 |  |
| 228 | 1 |  |  |  | 1 |  |
| 257 | 1 |  |  |  | 1 |  |
| Total | 350 | 219 | 31 | 28 | 34 | 38 |
| Span 8.0% or less | 80.5% | 96.7% | 93.5% | 78.6% | 67.6% | 92.1% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 111. Frequency distribution of species in range classes of relative length of the quadrate in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 13.0–20.9 | 9/9 | 6/5 | | | |
| 2 | 21.0–28.9 | 41/29 | 9/6 | 5/1 | | |
| 3 | 29.0–36.9 | 79/29 | 8/7 | 16/4 | 1/0 | 1/0 |
| 4 | 37.0–44.9 | 56/25 | 4/2 | 3/2 | 4/1 | 4/1 |
| 5 | 45.0–52.9 | 19/8 | 3/3 | 3/2 | 11/3 | 14/3 |
| 6 | 53.0–60.9 | 7/2 | | 1/0 | 10/3 | 13/2 |
| 7 | 61.0–68.9 | 4/0 | 1/1 | | 7/1 | 5/0 |
| 8 | 69.0–76.9 | 3/2 | | | 1/0 | 1/0 |
| 9 | 77.0–84.9 | 1/1 | | | | |
| Totals | | 219/105 | 31/24 | 28/9 | 34/8 | 38/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

## FAMILIAL RANGES OF VARIATION (Table 112)

Colubridae—This family has all three states in a sample from 369 skulls of 219 species of 105 genera. State I occurs in 195 species of 91 genera, II in 15 species of 5 genera, III in 9 species of 9 genera.

TABLE 112. Distribution of character states of the relative length of the quadrate.

| | STATES | | |
|---|---|---|---|
| | III | I | II |
| Classes[1] | 1 | 2–5 | 6–9 |
| | | SPECIES | |
| Colubridae —219 | 4.1% | 89.0% | 6.8% |
| Elapidae — 31 | 19.4 | 77.4 | 3.2 |
| Hydrophiidae— 28 | | 96.4 | 3.6 |
| Viperinae — 34 | | 47.1 | 52.9 |
| Crotalinae — 38 | | 50.0 | 50.0 |
| *Azemiops* — 1 | | 88.8 | |
| *Atractaspis* — 3 | | 66.7 | 33.3 |
| | | GENERA | |
| Colubridae —105 | 8.6 | 86.7 | 4.8 |
| Elapidae — 24 | 20.8 | 75.0 | 4.2 |
| Hydrophiidae— 9[2] | | 100.0 | |
| Viperinae — 8 | | 50.0 | 50.0 |
| Crotalinae — 6 | | 66.7 | 33.3 |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 1 | | 100.0 | |

[1] See Table 111.

[2] *Aipysurus* has States I and II.

The range of variation in the relative length of the quadrate is from 13.0 per cent (*Carphophis amoena*) to 84.6 per cent (*Grayia smithi*). The maximum span in a single species is 17.1 per cent (*Heterodon nasicus*). However, 96.7 per cent of the species have a span of 8.0 per cent or less.

Elapidae—This family has all three states in a sample from 47 skulls of 31 species of 24 genera. State I occurs in 24 species of 18 genera, II occurs in *Acanthophis antarcticus,* III in 6 species of 5 genera.

The range in the relative length of the quadrate is from 14.4 per cent (*Leptomicrurus collaris*) to 63.7 per cent (*Acanthophis antarcticus*). The maximum span in a single species is 16.4 per cent (*Ophiophagus hannah*). However, 93.5 per cent of the species have a span of 8.0 per cent or less.

Hydrophiidae—The sea snakes have States I and II in a sample from 66 skulls of 28 species of 9 genera. State I occurs in 27 species and 9 genera, II in *Aipysurus laevis.*

The range of variation in the relative length of the quadrate is from 24.2 per cent (*Hydrophis brookii*) to 55.4 per cent (*Aipysurus laevis*). The maximum span in a single species is 15.1 per cent (*Lapemis hardwickii*). However, 78.6 per cent of the species have a span of 8.0 per cent or less.

Viperinae—The true vipers have States I and II in a sample from 81 skulls of 34 species of the 8 genera. State I occurs in 16 species and 4 genera, II in 18 species and 4 genera.

The range of variation in the relative length of the quadrate is from 27.8 per cent (*Vipera berus*) to 82.3 per cent (*Bitis gabonica*). The maximum span in a single species is 25.7 per cent (*B. gabonica*). However, 67.6 per cent of the species have a span of 8.0 per cent or less.

Crotalinae—The pit vipers have States I and II in a sample from 63 skulls of 38 species of the 6 genera. State I occurs in 19 species and 4 genera, II in 19 species and 2 genera.

The range of variation in the relative length of the quadrate is from 33.8 per cent (*Agkistrodon strauchi*) to 74.3 per cent (*Trimeresurus wagleri*). The maximum span in a single species is 12.7 per cent (*Crotalus adamanteus*). However, 92.1 per cent of the species have a span of 8.0 per cent or less.

*Azemiops* has State I as sampled from 2 skulls: range is 27.3 per cent—31.8 per cent; span is 4.6 per cent.

*Atractaspis* has States I and II in a sample from 3 skulls of 3 species. The range of variation is from 47.4 per cent (*A. irregularis*) to 59.9 per cent (*A. microlepidota*).

## PHYLETICS OF CHARACTER 38

Character States II and III are rare in the colubrids (table 112) (Criterion 2).

State II, a relatively long quadrate, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Boiga blandingi*
- *Enhydris bocourti*
- *Grayia smithi*
- *Heterodon* (3)
- *Lystrophis semicinctus*
- *Macropisthodon rudis*
- *Natrix cyclopion*
  - *rhombifera*
  - *taxispilota*

  *Psammodynastes pictus*
  *Xenodon* (3)
Elapidae
  *Acanthophis antarcticus*
Hydrophiidae
  *Aipysurus laevis*
Viperinae
  *Atheris chlorechis*
    *nitschei*
    *squamiger*
  *Bitis* (8)
  *Causus defilippii*
    *rhombeatus*
  *Cerastes* (2)
  *Echis coloratus*
  *Vipera lebetina*
    *persica*
Crotalinae
  *Agkistrodon acutus*
    *bilineatus*
    *piscivorus*
    *rhodostoma*
  *Bothrops alternatus*
    *jararacussu*
    *schlegeli*
  *Crotalus adamanteus*
    *atrox*
    *durissus*
    *horridus*
    *mitchellii*
    *molossus*
    *ruber*
    *viridis*
  *Trimeresurus jerdoni*
    *puniceus*
    *sumatranus*
    *wagleri*
*Atractaspis microlepidota*

In these colubrids this character state has a higher frequency of correlation with derived states of 14 other characters compared to the frequency distribution of these states of the same 14 characters in the total working sample (table 113) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the terrestrial and aquatic habitats (53.3 per cent, 33.3 per cent) compared to the relative abundance of terrestrial and aquatic colubrid species in the total working sample (36.2 per cent, 14.9 per cent—table 114) (Criterion 5).

Almost all of these species live in, near, or over water and feed principally on frogs and fish. The elongation of the quadrate is interpreted as adaptive and probably functionally related to feeding on animals that are dependent on an aquatic environment (Criterion 4).

Genera of one notable taxonomic group appearing in the above list have been related to each other by various authors (H. M. Smith, 1964; Weaver, 1965) (Criterion 7). They are *Heterodon, Xenodon,* and *Lystrophis.* Underwood (1967, p. 103) summarized and pointed out discrepancies between various authors as to their reasons for grouping these genera, but he agreed as to their intergeneric relationships. The enlargement of the rear teeth or fangs is emphasized as well as the vertical movement (E. G. Boulenger, 1915) or lateral rotation (Weaver, 1965) of the maxilla and a diet of frogs. We are unaware of any functional analysis of the maxillary move-

TABLE 113. Correlation of States II and III of Character 38 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 38 | In species having State III of Character 38 | In total sample |
| 1 | 33.3% (3)* | 44.4% (4) | 14.3% (28) |
| 2 | 26.7 (2) | | 15.6 (31) |
| 7 | | 100.0 (9) | 25.5 (56) |
| 9 | 20.0 (1) | 33.3 (3) | 6.8 (14) |
| 11 | | 44.4 (4) | 26.7 (50) |
| 12 | 26.7 (2) | | 4.8 (13) |
| 16 | 60.0 (5) | | 21.7 (34) |
| 19 | | 100.0 (9) | 36.8 (68) |
| 22 | | 66.7 (6) | 4.5 (11) |
| 26 | 33.3 (5) | | 12.6 (19) |
| 27 | | 50.0 (4) | 17.9 (40) |
| 29 | | 50.0 (4) | 10.1 (27) |
| 31 | 40.0 (6) | 37.5 (3) | 19.5 (44) |
| 32 | | 57.1 (4) | 26.3 (55) |
| 33 | 60.0 (6) | | 43.0 (76) |
| 34 | | 50.0 (4) | 6.8 (18) |
| 35 | | 33.3 (3) | 2.0 ( 6 ) |
| 36 | | 33.3 (3) | 6.1 (16) |
| 37 | 53.3 (4) | | 22.9 (54) |
| 39 | 20.0 (2) | 55.6 (5) | 9.0 (15) |
| 40 | 53.3 (5) | 50.0 (4) | 24.8 (54) |
| 41 | 36.4 (4) | 50.0 (3) | 10.9 (20) |
| 42 | 36.4 (3) | 66.7 (4) | 8.7 (14) |
| 48 | 21.4 (2) | | 6.2 (11) |

* Number of genera.

TABLE 114. Habitat distribution of colubrid species having States II and III of Character 38 compared to the total colubrid working sample.

| | Total Working Sample % | State II Character 38 % | State III Character 38 % |
|---|---|---|---|
| Terrestrial | 36.2 | 53.3 | |
| Arboreal | 16.5 | 6.7 | |
| Aquatic | 14.9 | 33.3 | 11.1 |
| Subterrestrial | 10.8 | | 33.3 |
| Fossorial | 12.4 | | 55.6 |
| Variation | 5.3 | 6.7 | |
| Unknown | 3.5 | | |

ment of any other species mentioned above. However, it must be stressed that many of the above genera have greatly enlarged rear teeth (M. A. Smith, 1943, figs. 99A, 116A). Many of these other species also feed on frogs. It appears that polyphyletic grouping of these New World genera (Xenodontinae: Underwood, 1967) still remains a possibility.

The application of five criteria (2, 3, 4, 5, 7) strongly suggests that State II is derived (Criterion 8).

State III, a relatively short quadrate, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Abastor erythrogrammus*
  - *Calamaria pavimentata*
  - *Carphophis amoena*
  - *Chilorhinophis carpenteri*
  - *Geophis semidoliatus*
  - *Miodon gabonensis*
  - *Opisthotropis latouchi*
  - *Pseudorabdion longiceps*
  - *Tantilla gracilis*
- Elapidae
  - *Brachyurophis semifasciata*
  - *Elaps lacteus*
  - *Leptomicrurus collaris narducci*
  - *Micruroides euryzanthus*
  - *Vermicella annulata*

In these colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total working sample (table 113) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the subterrestrial and fossorial habitat (33.3 per cent, 55.6 per cent), compared to the relative abundance of subterrestrial and fossorial colubrid species in the total working sample (10.8 per cent, 12.4 per cent—table 114) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

State II probably arose in a different sequential direction than State III because State II correlates mostly with derived states of

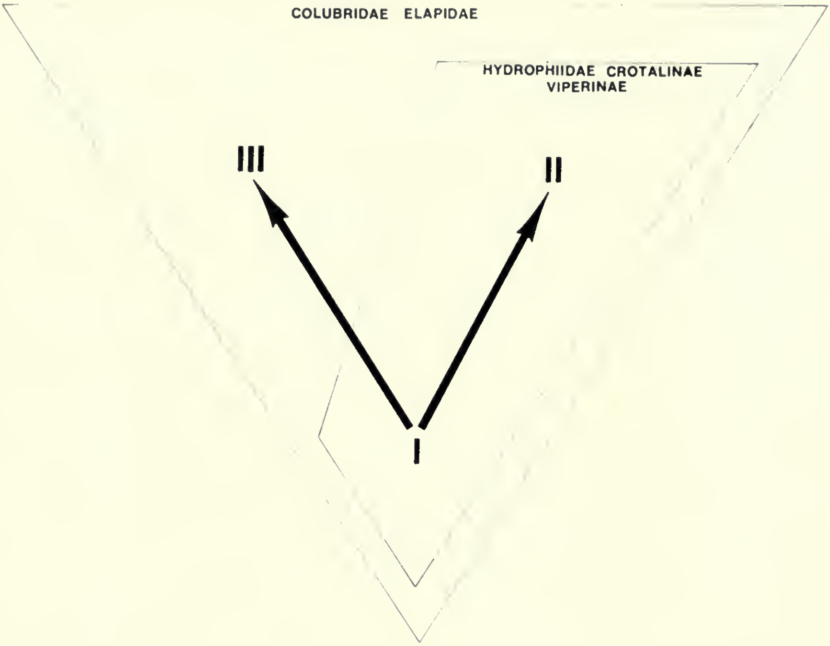

Fig. 37. Distribution among families of states of Character 38. Direction of change among states shown by arrows.

different characters (table 113) and is predominantly abundant in different habitat zones (table 114).

The serial nature of this character (i.e., numerical order—table 111, column 2) makes the arrangement given of the three designated states the most probable.

Our interpretation of the phyletics of Character 38 is shown in Figure 37.

## Character 39—Relative Length of Squamosal

### Description of Character

The relative length of the squamosal bone is here defined as the length of squamosal as a proportion of the total length of the skull. The squamosal has also been called the tabular (Bogert, 1943, figs. 17–19) or supratemporal (Romer, 1956, p. 573) in ophidian literature. See Peters (1964, pp. 347, 352) on the nomenclatural confusion concerning this particular bone.

TABLE 115. Spans in relative length of squamosal by species and families.

|  |  | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 232 | 154 | 21 | 16 | 17 | 26 |
| 4 | 1 |  | 1 |  |  |  |
| 6 | 2 | 2 |  |  |  |  |
| 8 | 1 |  |  |  |  | 1 |
| 9 | 3 | 2 |  |  | 1 |  |
| 10 | 1 | 1 |  |  |  |  |
| 11 | 2 |  | 1 |  | 1 |  |
| 12 | 2 | 1 |  | 1 |  |  |
| 13 | 2 | 2 |  |  |  |  |
| 14 | 1 |  |  | 1 |  |  |
| 15 | 1 |  | 1 |  |  |  |
| 16 | 2 | 2 |  |  |  |  |
| 17 | 6 | 3 | 1 |  |  | 2 |
| 18 | 3 | 2 | 1 |  |  |  |
| 19 | 1 | 1 |  |  |  |  |
| 20 | 3 | 3 |  |  |  |  |
| 21–30 | 16 | 4 | 3 | 3 | 3 | 3 |
| 31–40 | 11 | 7 |  | 1 | 1 | 2 |
| 41–50 | 14 | 9 | 1 | 1 | 1 | 2 |
| 51–60 | 13 | 9 |  |  | 3 | 1 |
| 61–70 | 11 | 6 | 1 | 2 | 2 |  |
| 71–80 | 12 | 7 | 1 | 1 | 3 |  |
| 81–90 | 4 | 3 |  | 1 |  |  |
| 91–100 | 5 | 3 |  |  | 1 | 1 |
| 104–107 | 2 | 2 |  |  |  |  |
| 111 | 2 | 1 |  |  | 1 |  |
| 126 | 1 | 1 |  |  |  |  |
| 162–166 | 3 | 2 |  | 1 |  |  |
| 216 | 1 | 1 |  |  |  |  |
| Totals | 358 | 228 | 32 | 28 | 34 | 38 |
| Span 7.0% or less | 91.6% | 91.2% | 96.9% | 92.6% | 85.3% | 97.4% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 116. Frequency distribution of species in range classes of relative length of the squamosal in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 3.3–10.2 | 2/2 | | | | |
| 2 | 10.3–17.2 | 6/4 | 3/2 | | | |
| 3 | 17.3–24.2 | 27/20 | 10/7 | | 1/0 | 18/3 |
| 4 | 24.3–31.2 | 57/33 | 6/6 | 16/6 | 21/4 | 19/3 |
| 5 | 31.3–38.2 | 77/36 | 10/7 | 6/2 | 9/4 | 1/0 |
| 6 | 38.3–45.2 | 47/20 | 2/2 | 6/2 | 3/0 | |
| 7 | 45.3–52.2 | 9/4 | 1/1 | | | |
| 8 | 52.3–59.2 | 3/1 | | | | |
| Totals | | 228/120 | 32/25 | 28/10 | 34/8 | 38/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

## CLASSES AND STATES

The total range of variation in relative length of the squamosal was segmented by steps of 7.0 per cent since a span of 7.0 per cent covered most of the intraspecific variation encountered (91.6 per cent—table 115). Eight classes resulted as shown in Table 116. The mean of each taxon was assigned to a class (Table 116). States are established when there is a marked change in frequency of number of species between classes.

Three states are recognized:

State I —Classes 3–6 (17.3–45.2 per cent)
State II —Classes 7–8 (45.3–59.2)
State III—Classes 1–2 (3.3–17.2)

## FAMILIAL RANGES OF VARIATION (Table 117)

Colubridae—This family has all three states in a sample from 387 skulls of 228 species of 120 genera. State I occurs in 208 species of 110 genera, II in 12 species of 6 genera, III in 8 species of 4 genera.

The range in the relative length of the squamosal is from 3.3 per cent (*Aparallactus werneri*) to 57.7 per cent (*Natrix cyclopion*). The maximum span in a single species is 21.6 per cent (*Natrix cyclopion*).

TABLE 117. Distribution of character states of the relative length of the squamosal.

| | | STATES | |
|---|---|---|---|
| | I | II | III |
| Classes[1] | 3–6 | 7–8 | 1–2 |
| | | SPECIES | |
| Colubridae —228 | 91.2% | 5.3% | 3.5% |
| Elapidae — 32 | 87.5 | 3.1 | 9.4 |
| Hydrophiidae— 28 | 100.0 | | |
| Viperinae — 34 | 100.0 | | |
| Crotalinae — 38 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 2 | 100.0 | | |
| | | GENERA | |
| Colubridae —120 | 90.8 | 4.2 | 5.0 |
| Elapidae — 25 | 88.0 | 4.0 | 8.0 |
| Hydrophiidae— 10 | 100.0 | | |
| Viperinae — 8 | 100.0 | | |
| Crotalinae — 6 | 100.0 | | |
| *Azemiops* — 1 | 100.0 | | |
| *Atractaspis* — 1 | 100.0 | | |

[1] See Table 116.

However, 91.2 per cent of the species have a span of 7.0 per cent or less.

Elapidae—This family has all three states in a sample from 50 skulls of 32 species of 25 genera. State I occurs in 28 species of 22 genera, II in *Ophiophagus hannah,* III in 3 species of 2 genera.

The range in the relative length of the squamosal is from 12.1 per cent (*Leptomicrurus narducci*) to 48.2 per cent (*Ophiophagus hannah*). The maximum span in a single species is 7.8 per cent (*Naja naja*). However, 96.9 per cent of the species have a span of 7.0 per cent or less.

Hydrophiidae—The sea snakes only have State I in a sample from 68 skulls of 28 species of 10 genera.

The range in the relative length of the squamosal is from 24.6 per cent (*Pelamis platurus*) to 51.9 per cent (*Laticauda colubrina*). The maximum span in a single species is 16.6 per cent (*L. colubrina*). However, 92.6 per cent of the species have a span of 7.0 per cent or less.

Viperinae—The true vipers only have State I in a sample from 81 skulls of 34 species of the 8 genera.

The range in the relative length of the squamosal is from 22.7 per cent (*Atheris hindii*) to 42.6 per cent (*Causus rhombeatus, Vipera ammodytes*). The maximum span in a single species is 11.1 per cent (*Causus rhombeatus*). However, 85.3 per cent of the species have a span of 7.0 per cent or less.

Crotalinae—The pit vipers only have State I in a sample from 63 skulls of 38 species of the 6 genera.

The range in the relative length of the squamosal is from 24.4 per cent (*Trimeresurus stejnegeri*) to 38.3 per cent (*T. monticola*). The maximum span in a single species is 9.4 per cent (*Crotalus lepidus*). However, 97.4 per cent of the species have a span of 7.0 per cent or less.

*Azemiops* has State I as sampled from 2 skulls: range is 26.8–28.3 per cent; span is 1.6 per cent.

*Atractaspis* only has State I in a sample from 3 skulls of 2 species. The range of variation is 28.0 per cent (*A. microlepidota*) to 30.7 per cent (*A. microlepidota*); span of 2.8 per cent.

### PHYLETICS OF CHARACTER 39

Character States II and III are rare in the colubrids (table 117) (Criterion 2).

State II, a relatively long squamosal, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
*Cyclagras gigas*
*Enhydris chinensis*
*enhydris*
*Homalopsis buccata*
*Macropisthodon rudis*
*Natrix aequifasciata*
*cyclopion*
*rhombifera*
*taxispilota*
*Pseudaspis cana*
*Thamnophis eques*
*Xenodon merremii*
Elapidae
*Ophiophagus hannah*

In these colubrids this character state has a higher frequency of correlation with derived states of seven other characters compared to the frequency distribution of these states of the same seven characters in the total sample (table 118) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the aquatic habitat (75.0 per cent) compared to the rela-

TABLE 118. Correlation of States II and III of Character 39 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 39 | In species having State III of Character 39 | In total working sample |
| 1 | 25.0% (2)* | 37.5% (2) | 14.3% (28) |
| 7 | | 100.0 (6) | 25.5 (56) |
| 9 | | 50.0 (3) | 6.8 (14) |
| 11 | | 50.0 (3) | 26.7 (50) |
| 13 | | 62.5 (3) | 31.8 (54) |
| 16 | 66.7 (5) | | 21.7 (34) |
| 17 | 58.3 (4) | | 35.4 (48) |
| 19 | | 100.0 (6) | 36.8 (68) |
| 22 | | 50.0 (3) | 4.5 (11) |
| 27 | | 50.0 (3) | 17.9 (40) |
| 28 | | 57.1 (3) | 11.7 (26) |
| 29 | | 37.5 (4) | 10.1 (27) |
| 31 | 33.3 (4) | 66.7 (4) | 19.5 (44) |
| 32 | | 100.0 (4) | 26.3 (55) |
| 34 | | 66.7 (4) | 6.8 (18) |
| 36 | | 42.9 (3) | 6.1 (16) |
| 37 | 66.7 (5) | | 22.9 (54) |
| 38 | 41.7 (3) | 71.4 (5) | 16.2 (27) |
| 40 | | 42.9 (3) | 24.8 (54) |
| 42 | 27.3 (2) | 71.4 (4) | 8.7 (14) |
| 44 | | 42.9 (3) | 5.8 (11) |
| 46 | | 50.0 (3) | 26.9 (52) |
| 49 | | 37.5 (2) | 15.5 (26) |

* Number of genera.

TABLE 119. Habitat distribution of colubrid species having States II and III of Character 39 compared to the total colubrid sample.

| | Total Working Sample % | State II Character 39 % | State III Character 39 % |
|---|---|---|---|
| Terrestrial | 36.2 | 16.7 | |
| Arboreal | 16.5 | | |
| Aquatic | 14.9 | 75.0 | |
| Subterrestrial | 10.8 | | 12.5 |
| Fossorial | 12.4 | 8.3 | 87.5 |
| Variation | 5.3 | | |
| Unknown | 3.5 | | |

tive abundance of aquatic colubrid species in the total sample (14.9 per cent—table 119) (Criterion 5).

The striking similarity that almost all (not monotypic *Pseudaspis*) these species have in common is their occurrence in aquatic habitats and their diets of frogs and/or fish. The long squamosal is interpreted as an adaptive state related to feeding (Criterion 4).

The application of four criteria (2, 3, 4, 5) strongly suggests that State II is derived (Criterion 8).

Species with a long dentary (Character 42) or quadrate (Character 38) are adapted in the same fashion as species with a long squamosal. However, only two species are common to the three lists of species with elongation of these three bones (*Natrix rhombifera, N. taxispilota*); four species of 12 have both a long quadrate and squamosal, and three of 12 have elongated dentary and squamosal. Elongation of these bones is thus not necessarily correlated. Probably elongation in one or more component(s) of this osteological arc (supratemporal-quadrate-mandible) is adaptive in facilitating grasping and/or engulfing aquatic prey, but the particular component varies from taxon to taxon. See Character 38 for further discussion.

State III, a relatively short squamosal, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Abastor erythrogrammus*
  - *Aparallactus lunulatus*
    - *werneri*
  - *Calamaria pavimentata*
    - *septentrionalis*
  - *Chilorhinophis carpenteri*
  - *Miodon gabonensis*
  - *Pseudorabdion longiceps*
- Elapidae
  - *Elaps lacteus*
  - *Leptomicrurus* (2)

In these colubrids this character state has a higher frequency of correlation with derived states of 20 other characters compared to the

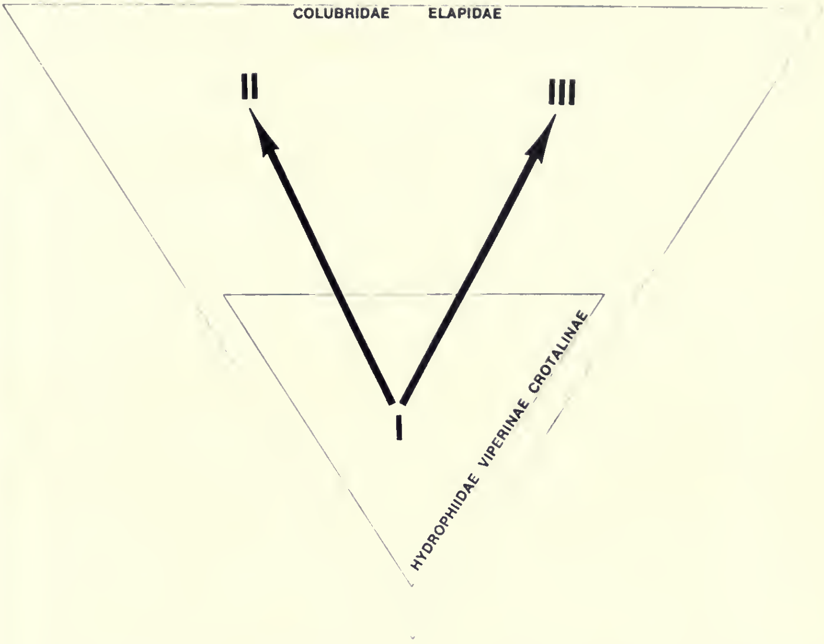

FIG. 38. Distribution among families of states of Character 39. Direction of change among states shown by arrows.

frequency distribution of these states of the same 20 characters in the total sample (table 118) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the fossorial habitat (87.5 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent) (table 119) (Criterion 5).

Seven of these eight species belong to two subgroups: Aparallactinae and Calamarinae (Inger and Marx, 1965, table 58) (Criterion 7).

The application of four criteria (2, 3, 5, 7) suggests that State III is derived (Criterion 8).

State II probably arose in a different sequential direction from State III because State II correlates mostly with derived states of different characters (table 118) and is predominantly abundant in different habitat zones (table 119).

The nature of this character (i.e., linearly ordered by size—table 116, column 2) makes the arrangement given of the three designated states the most probable.

Our interpretation of the phyletics of Character 39 is shown in Figure 38.

The vast majority of species and genera of colubrids and elapids have moderate-sized squamosals. All the vipers and sea snakes also have moderate-sized squamosals (table 116).

This retention of the primitive state in derived stocks obviously offers no phylogenetic information within these stocks. Of the four segments of the mandibular arc (Characters 38, 39, 41, 42) only in the squamosal is there failure to diverge substantially from the central tendency of the colubrids (tables 112, 117, 127, 132). The two more distal units show substantially more variation and divergence than the proximal two.

## Character 40—Compound Processes

### Description of Character

Posteriorly, the compound bone usually has one or two dorsal vanes along the longitudinal axis of the mandible. The compound has been called the articular bone (Guibé, 1970, fig. 92) and the angular (Radovanovic, 1937) and the compound processes have been called lateral bony leaves (Radovanovic, *ibid.*). The medial process at least probably represents the fused surangular.

Six states are recognized:

State I —process absent
State II —one process, lateral
State III—one process, medial
State IV—two processes, equal size
State V —two processes, lateral larger
State VI—two processes, medial larger

### Familial Ranges of Variation (Table 120)

Colubridae—This family has all six states in a sample of 312 species of 164 genera (561 skulls). State I occurs in 16 species of 11 genera (20 skulls), II in 9 species of 6 genera (16 skulls), III in 234 species of 126 genera (417 skulls), IV in 16 species of 14 genera (41 skulls), V in 2 species of 2 genera (7 skulls), VI in 35 species of 26 genera (60 skulls).

Intrageneric variation occurs in 18 genera: *Drymobius, Elaphe, Helicops, Masticophis, Oxybelis, Psammodynastes, Pseustes, Tele-*

TABLE 120. Distribution of character states of the compound processes.

| | STATES | | | | | | |
|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | |
| Description | Absent | One, lateral | One, medial | Two, equal size | Two, lateral larger | Two, medial larger | |
| | | | SPECIES | | | | |
| Colubridae —312 | 5.1% | 2.9% | 75.0% | 5.1% | 0.6% | 11.2% | |
| Elapidae — 68 | 42.6 | 23.5 | 30.9 | 1.5 | | 1.5 | |
| Hydrophiidae— 41 | 61.0 | 7.3 | 22.0 | 7.3 | | 2.4 | |
| Viperinae — 34 | | | 85.3 | 8.8 | | 5.9 | |
| Crotalinae — 45 | | | 100.0 | | | | |
| *Azemiops* — 1 | | | 100.0 | | | | |
| *Atractaspis* — 5 | 100.0 | | | | | | |
| | | | GENERA | | | | INTRAGENERIC VARIATION* |
| Colubridae —164 | 3.0 | 3.0 | 66.5 | 6.1 | 1.2 | 9.1 | 11.0% |
| Elapidae — 37 | 32.4 | 32.4 | 16.2 | | | 2.7 | 16.2 |
| Hydrophiidae— 16 | 43.8 | | 25.0 | | | 6.3 | 25.0 |
| Viperinae — 8 | | | 87.5 | | | | 12.5 |
| Crotalinae — 6 | | | 100.0 | | | | |
| *Azemiops* — 1 | | | 100.0 | | | | |
| *Atractaspis* — 1 | 100.0 | | | | | | |

* Colubridae: III, VI=9 genera; III, I=4; III, IV=1; III, IV, VI=1; III, IV, VI, I=1; III, II=1; IV, I=1. Elapidae: III, I=3; II, I=2; III, IV=1. Hydrophiidae: IV, I=1; II, I=2; I, III, IV=1. Viperinae: IV, VI=1.

*scopus, Xenodon* (III, VI); *Aparallactus, Atractus, Chilomeniscus, Natrix* (I, III); *Leptophis* (III, IV); *Calamaria* (III, IV, VI); *Boiga* (I, III, IV, VI); *Geophis* (II, III); *Conopsis* (I, IV).

Elapidae—This family has States I, II, III, IV, and VI in a sample of 68 species of 37 genera (109 skulls). State I occurs in 29 species of 17 genera (56 skulls), II in 16 species of 14 genera (20 skulls), III in 21 species of 10 genera (27 skulls), IV in *Denisonia superba* (4 skulls), VI in *Boulengerina annulata* (2 skulls).

Intrageneric variation occurs in 6 genera: *Hoplocephalus, Micropechis, Micrurus* (III, I); *Demansia, Pseudechis* (II, I); *Denisonia* (III, IV).

Hydrophiidae—The sea snakes have States I, II, III, IV, and VI in a sample of 41 species of the 16 genera (140 skulls). State I occurs in 25 species of 11 genera (79 skulls), II in 3 species of 2 genera (8 skulls), III in 9 species of 5 genera (33 skulls), IV in 3 species of 2 genera (5 skulls), VI in monotypic *Pelamis* (2 skulls).

Intrageneric variation occurs in 4 genera: *Laticauda, Microcephalophis* (I, II); *Aipysurus* (I, IV); *Hydrophis* (I, III, IV).

Viperinae—The true vipers have States III, IV, and VI in a sample of 34 species of the 8 genera (95 skulls). State III occurs in 29 species of 7 genera (84 skulls), IV in 3 species of *Causus* (9 skulls), VI in 2 species of *Causus* (2 skulls).

Intrageneric variation occurs in *Causus* (IV, VI).

Crotalinae—The pit vipers only have State III in a sample of 45 species of the 6 genera (82 skulls).

*Azemiops* has State III (2 skulls).

*Atractaspis* has State I in a sample of 5 species (8 skulls).

## PHYLETICS OF CHARACTER 40

Character State III is common in the colubrids (75.0 per cent—table 120). For these colubrids this character state does not have a higher frequency of correlation with derived states of any of the 49 other characters compared to the frequency distribution of these states of the same 49 characters in the total sample (table 121).

Also this state does not have a significantly larger number of species confined to a geographic range compared to the relative abundance of colubrid species in the total sample (table 122).

In addition, colubrid species having State III do not have a significantly larger number of species confined to any particular habitat

TABLE 121. Correlation of State III of Character 40 with derived states of the other characters in Colubridae.

| Character | Frequency of derived states in indicated characters— | |
|---|---|---|
| | In species having State III of Character 40 | In total working sample |
| 1 | 12.0% (17)* | 14.3% (28) |
| 2 | 12.8 (22) | 15.6 (31) |
| 3 | 0 | 0.1 (3) |
| 4 | 3.4 (3) | 3.8 (4) |
| 5 | 1.7 (4) | 3.5 (9) |
| 6 | 0 | 0 |
| 7 | 20.5 (30) | 25.5 (56) |
| 8 | 0 | 0 |
| 9 | 3.5 (6) | 6.8 (14) |
| 10 | 0 | 0.6 (1) |
| 11 | 26.7 (34) | 26.7 (50) |
| 12 | 3.8 (9) | 4.8 (13) |
| 13 | 29.9 (43) | 31.8 (54) |
| 14 | 1.3 (3) | 3.5 (7) |
| 15 | 0 | 0 |
| 16 | 22.6 (27) | 21.7 (34) |
| 17 | 36.8 (38) | 35.4 (48) |
| 18 | 0 | 0.1 (3) |
| 19 | 36.5 (52) | 36.8 (68) |
| 20 | 38.0 (51) | 41.2 (74) |
| 21 | 19.9 (22) | 18.9 (29) |
| 22 | 2.6 (5) | 4.5 (11) |
| 23 | 1.7 (3) | 1.9 (5) |
| 24 | 2.6 (6) | 3.8 (11) |
| 25 | 5.9 (9) | 6.3 (12) |
| 26 | 11.8 (14) | 12.6 (19) |
| 27 | 14.9 (27) | 17.9 (40) |
| 28 | 8.8 (17) | 11.7 (26) |
| 29 | 5.8 (13) | 10.1 (27) |
| 30 | 5.6 (10) | 6.3 (15) |
| 31 | 20.3 (34) | 19.5 (44) |
| 32 | 20.9 (35) | 26.3 (55) |
| 33 | 39.1 (55) | 43.0 (76) |
| 34 | 5.3 (11) | 6.8 (18) |
| 35 | 0.4 (1) | 2.0 (6) |
| 36 | 3.4 (7) | 6.1 (16) |
| 37 | 21.4 (41) | 22.9 (54) |
| 38 | 12.7 (18) | 16.2 (27) |
| 39 | 8.9 (11) | 9.0 (15) |
| 41 | 2.0 (12) | 10.9 (20) |
| 42 | 6.1 (8) | 8.7 (14) |
| 43 | 1.7 (2) | 1.9 (3) |
| 44 | 5.4 (8) | 5.8 (11) |
| 45 | 21.8 (16) | 19.5 (21) |
| 46 | 27.1 (39) | 26.9 (52) |
| 47 | 46.1 (58) | 48.5 (84) |
| 48 | 5.3 (7) | 6.2 (11) |
| 49 | 15.1 (18) | 15.5 (26) |
| 50 | 18.5 (19) | 20.0 (24) |

* Number of genera.

TABLE 122. Geographic distribution of colubrid species having State III of Character 40 compared to the total colubrid sample.

| | Total working sample | Character 40 State III |
|---|---|---|
| United States | 17.2% | 16.7% |
| South America | 17.8 | 17.5 |
| Central America | 6.7 | 8.1 |
| Mexico | 7.0 | 5.1 |
| Caribbean | 3.5 | 4.7 |
| New World, intraregional | 1.9 | 1.7 |
| Tropical Africa | 14.3 | 14.1 |
| Northern Africa & Sahara | 1.3 | 1.7 |
| Europe | 1.6 | 2.1 |
| Southwestern Asia & Pakistan | 2.5 | 2.6 |
| India, Ceylon, Nepal | 2.9 | 2.1 |
| Eastern Asia | 10.8 | 12.8 |
| Southeastern Asia | 1.9 | 1.7 |
| Indo-Australian, Phil. Ids. | 4.8 | 3.4 |
| Moluccan | 0.6 | 0.4 |
| New Guinea-New Britain | 0.6 | 0.4 |
| Madagascar | 1.3 | 1.3 |
| Old World, intraregional | 3.2 | 3.4 |
| Total number of species | 314 | 234 |

zone compared to the relative abundances of colubrid species in the total sample (table 123).

Therefore we conclude that there are no phyletic criteria applicable to State III, and this state is primitive.

State I is rare in the colubrids (table 120) (Criterion 2). State I, absence of compound process, occurs in the following colubrids (plus other taxa):

Colubridae
- *Aparallactus lunulatus*
- *Apostolepis ambinigra*
- *Atractus elaps*
  - *latifrons*
  - *ventrimaculatus*
- *Boiga jaspidea*
- *Chilomeniscus cinctus*
- *Chilorhinophis carpenteri*
- *Conopsis lineatus*
- *Elachistodon westermanni*
- *Natrix piscator*
  - *stolata*
  - *valida*
- *Sonora episcopa*
  - *semiannulata*
- *Stilostoma extenuatum*

Elapidae
- *Aspidelaps lubricus*
  - *scutatus*
- *Brachyurophis semifasciata*
- *Bungarus candidus*
  - *fasciatus*
  - *multicinctus*
- *Cacophis harriettae*
- *Demansia textilis*
- *Elapsoidea sundevalli*
- *Hemachatus haemachatus*
- *Hoplocephalus bungaroides*
- *Micropechis elapsoides*
- *Micrurus affinis*
  - sp.
- *Naja flava*
  - *haje*

*melanoleuca*
*naja*
*nigricollis*
*nivea*
*Ophiophagus hannah*
*Pseudechis australis*
*porphyriacus*
*Pseudohaje goldii*
*nigra*
*Toxicocalamus stanleyanus*
*Vermicella annulata*
*Walterinnesia aegyptia*
Hydrophiidae
*Acalyptophis*
*Aipysurus apraefrontalis*
*duboisii*
*foliosquama*
*laevis*
*Emydocephalus annulatus*
*Hydrophis brookii*
*caerulescens*
*fasciatus*
*inornatus*
*klossi*
*lapemoides*
*melanocephalus*
*melanosoma*
*mertoni*
*torquatus*
*Kerilia*
*Kolpophis*
*Lapemis*
*Laticauda colubrina*
*laticaudata*
*Microcephalophis cantoris*
*Thalassophina*
*Thalassophis*
*Atractaspis*

In these colubrids, State I has a higher frequency of correlations with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total sample (table 124) (Criterion 3).

Also these colubrids have a larger number of species confined to the fossorial habitat (62.5 per cent) compared to the abundance of fossorial colubrid species in the total sample (12.4 per cent—table 123) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

TABLE 123. Habitat distribution of colubrid species having certain states of Character 40 compared to the total colubrid sample.

| | Total working sample | CHARACTER 40 STATES III | II | IV | I | VI |
|---|---|---|---|---|---|---|
| Terrestrial | 36.2% | 40.2% | 22.2% | 25.0% | 6.3% | 34.3% |
| Arboreal | 16.5 | 16.7 | 33.3 | 31.3 | 6.3 | 11.4 |
| Aquatic | 14.9 | 17.5 | | 6.3 | 12.5 | |
| Subterrestrial | 10.8 | 10.7 | 11.1 | 12.5 | 6.3 | 11.4 |
| Fossorial | 12.4 | 6.8 | 33.3 | 25.0 | 62.5 | 11.4 |
| Variation | 5.3 | 3.8 | | | | 25.7 |
| Unknown | 3.5 | 4.3 | | | 6.3 | |
| Total no. of species* | 314 | 234 | 9 | 16 | 16 | 35 |

* Data omitted on two species of State V and lacking on two species lacking complete skulls.

TABLE 124. Correlation of States I, II, IV, and VI of Character 40 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State I of Character 40 | In species having State II of Character 40 | In species having State IV of Character 40 | In species having State VI of Character 40 | In total working sample |
| 1 | | | 31.3% (3) | | 14.3% (28) |
| 2 | | | 31.3 (3) | | 15.6 (31) |
| 7 | 62.5% (8)* | 66.7% (4) | | | 25.5 (56) |
| 9 | 18.8 (3) | | 25.0 (2) | 14.3% (5) | 6.8 (14) |
| 11 | | | | 41.2 (12) | 26.7 (50) |
| 12 | | | 18.8 (1) | | 4.8 (13) |
| 13 | | 77.8 (5) | | | 31.8 (54) |
| 14 | 18.8 (2) | | 25.0 (2) | | 3.5 (7) |
| 16 | | 33.3 (1) | 31.3 (3) | | 21.7 (34) |
| 18 | | 33.3 (1) | | | 0.1 (3) |
| 20 | | 55.6 (3) | | 54.3 (16) | 41.2 (74) |
| 22 | | | | 14.3 (4) | 4.5 (4) |
| 24 | | | | 11.4 (4) | 3.8 (4) |
| 27 | | 57.1 (3) | | | 17.9 (40) |
| 28 | | | 25.0 (4) | | 11.7 (26) |
| 29 | 35.7 (4) | 62.5 (3) | 18.8 (3) | | 10.1 (27) |
| 32 | 76.9 (6) | 66.7 (4) | | | 26.3 (55) |
| 33 | | | | 71.4 (18) | 43.0 (76) |
| 34 | | 28.6 (2) | | | 6.8 (18) |
| 35 | | 25.0 (2) | | | 2.0 (6) |
| 36 | 20.0 (3) | 44.4 (3) | | | 6.1 (16) |
| 37 | | 55.6 (4) | | | 22.9 (54) |
| 38 | | 42.9 (3) | 40.0 (2) | | 16.2 (27) |
| 42 | 30.8 (3) | | | | 8.7 (14) |
| 44 | | 42.9 (2) | | | 5.8 (11) |
| 46 | 43.8 (5) | | | | 26.9 (52) |
| 50 | 42.9 (3) | | | | 20.0 (24) |

* Number of genera.

Character State II is rare in the colubrids (table 120) (Criterion 2).

State II, one lateral compound process, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Ficimia publia*
  - *Geophis semidoliatus*
  - *Lycodon aulicus*
    - *striatus*
  - *Miodon gabonensis*
  - *Prosymna ambigua*
- Elapidae
  - *Aspidomorphus lineaticollis*
    - *muelleri*
  - *Calliophis japonicus*
  - *Demansia olivacea*
  - *Elapognathus minor*
  - *Elaps lacteus*
  - *Furina diadema*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Maticora bivirgata*
  - *Micruroides euryxanthus*
  - *Micrurus fulvius*
  - *Ogmodon vitianus*
  - *Oxyuranus scutellatus*
  - *Parapistocalamus hedigeri*
  - *Pseudechis papuanus*
  - *Ultrocalamus preussi*
- Hydrophiidae
  - *Laticauda schistorhynchus*
    - *semifasciata*
  - *Microcephalophis gracilis*

In these colubrids this character state has a higher frequency of correlation with derived states of 14 other characters compared to the frequency distribution of these states of the same 14 characters in the total sample (table 124) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the arboreal and fossorial habitats (66.6 per cent) compared to the relative abundance of arboreal and fossorial colubrid species in the total sample (28.9 per cent—table 123) (Criterion 5).

In addition, these colubrids have a larger number of species confined to tropical Africa (55.6 per cent—five species) compared to the relative abundance of tropical African colubrids in the total sample (14.1 per cent) (Criterion 6).

The application of four criteria (2–3, 5–6) strongly suggests that this state is derived (Criterion 8).

Character State IV is rare in the colubrids (table 120) (Criterion 2).

State IV, two compound processes of equal size, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Boiga pulverulentus*
  - *Calamaria schlegeli*
  - *Cemophora coccinea*
  - *Conopsis nasus*
  - *Grayia smithi*

*Heterodon nasicus*
  *platyrhinos*
  *simus*
*Leptophis mexicanus*
*Oxyrhabdium modestum*
*Rhacidelus brazili*
*Rhynocalamus melanocephalus*
*Sibon sibon*
*Sibynomophus turgidus*
*Siphlophis cervinus*
*Stenorhina degenhardti*
Elapidae
  *Denisonia superba*
Hydrophiidae
  *Aipysurus eydouxi*
    *fuscus*
  *Hydrophis belcheri*
Viperinae
  *Causus defilippii*
    *resimus*
    *rhombeatus*

In these colubrids this character state has a higher frequency of correlation with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total sample (table 124) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the arboreal and fossorial habitats (56.3 per cent) compared to the relative abundance of arboreal and fossorial colubrid species in the total sample (28.9 per cent—table 123) (Criterion 5).

The application of three criteria (2–3, 5) suggests that this state is derived (Criterion 8).

Character State VI is moderately rare in the colubrids (table 120) (Criterion 2).

State VI, two compound processes—medial larger, occurs in the following colubrids (plus other taxa):

Colubridae
  *Aspidura trachyprocta*
  *Boiga blandingi*
  *Brachyorrhus albus*
  *Calamaria linnaei*
  *Chionactis occipitalis*
  *Chrysopelea ornata*
  *Drymarchon corais*
  *Drymobius bifossatus*
  *Elaphe frenatus*
  *Helicops schistosus*
  *Holuropholis olivaceus*
  *Homalopsis buccata*
  *Lioheterodon madagascariensis*
  *Masticophis flagellum*
  *Oxybelis fulgidus*
  *Psammodynastes pictus*
  *Pseudorhabdion collaris*
  *Pseustes sulphureus*
  *Pythonodipsas carinata*
  *Salvadora bairdi*
    *grahami*
    *hexalepis*
    *lemiscata*
    *lineata*
    *mexicana*
  *Stegonotus borneensis*
    *magnus*
  *Telescopus iberus*
  *Tropidocloniom lineatum*
  *Tropidodipsas fischeri*
    *philippi*
  *Xenodon colubrinus*
    *severus*
  *Zaocys dhumnades*
    *nigromarginatus*
Elapidae
  *Boulengerina annulata*

| | |
|---|---|
| Hydrophiidae | Viperinae |
| *Pelamis* | *Causus lichtensteini* |
| | *lineatus* |

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 124) (Criterion 3).

The application of two criteria (2–3) suggests that this state is derived (Criterion 8).

Character State V, restricted to the Colubridae, is extremely rare and is therefore considered derived (table 120) (Criterion 2). State V, two compound processes, lateral larger, only occurs in *Dryocalamus davisoni* and *Tantilla gracilis* (Criterion 2).

Given that a single, medial vane (III) is the primitive state and that no vanes (I) or a single, lateral vane (II) are derivative states, the relationships among these and intermediate conditions appear to follow logical courses. One course is simply reduction to a no-process condition. This evidently can take place directly from the primitive state, but may also be the end result after other morphotypes have been tried.

A shift directly from single medial to single lateral process is unlikely, for it involves considerable readjustments of mandibular musculature and feeding mechanics. More likely is a gradual replacement through development of the lateral process: at first a lesser partner of the medial process (VI), then an equal (IV), then a greater partner by virtue of the diminution or disappearance of the medial and/or continued growth of the lateral (V, II).

This suggested course is supported by the variation in the frequencies of habitat categories and in the correlations with derived states of other characters. The taxa exhibiting State VI, with a large medial process and a smaller lateral one, occur in the major habitat categories in practically identical proportions to the whole sample distribution, except for an unusually high percentage of mixed classification. In contrast, State IV and State II show significantly fewer terrestrial and more fossorial forms than the whole sample. As compared to States IV and II, State VI taxa show fewer derived state correlations (6 *versus* 9 for State IV and 14 for State II). State VI is also more closely linked to State III in terms of intrageneric variation.

Between States IV and II, the data support the notion that II, a single lateral process, is more derived. Both groups show a high proportion of odd digging taxa, as well as bird egg eaters and other arboreal forms.

State I is evidently strongly correlated with fossorial habits and morphology. As indicated by intrageneric variation in the elapids and colubrids, it may stem directly from State III. But it may also arise from another derived state(s?), as especially suggested by intrageneric variation in the elapids and hydrophiids. Since they may come in part from a relatively "generalized" group, as represented by the State III taxa, State I taxa as a group may not show as derivative an overall morphology as State II taxa. This is indeed the case (table 124). It is of interest that six of State I's nine derived state character correlates are among skeletal features, about the same proportion as for State II taxa, which have a total of 14 derived state character correlates. In two of four derived state characters common to both, State II taxa are distinctly the more derived group; in the other two cases, States II and I are approximately equal.

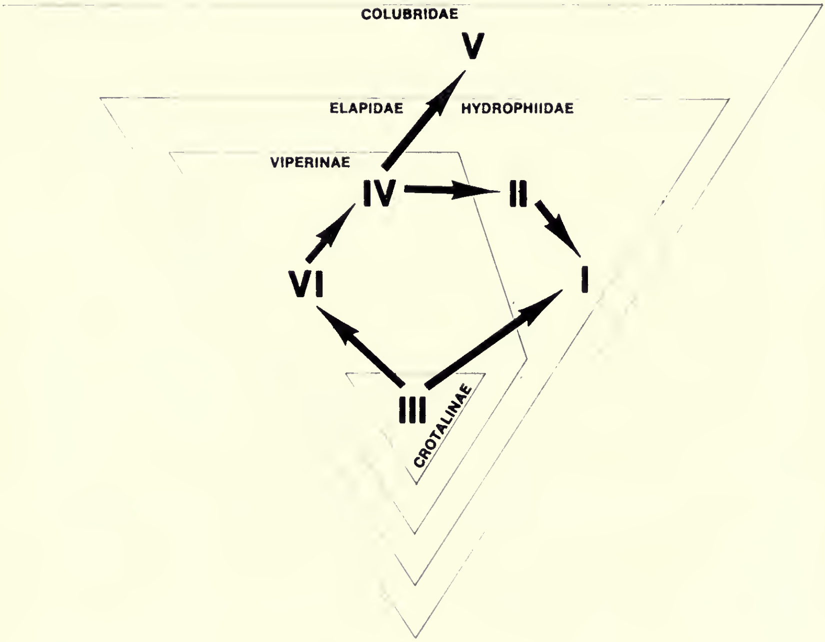

FIG. 39. Distribution among families of states of Character 40. Direction of change among states shown by arrows.

State V occurs only in two colubrid taxa, both subterrestrial. Its placement in the general phyletic scheme for the states (fig. 39) is primarily based on the logical morphological progression described above. The absence of this state in the elapids and hydrophiids and its extreme rarity in the colubrids suggests that it is a very transitory stage and for our purposes can be considered off the main sequence.

Our interpretation of the phyletics of Character 40 is shown in Figure 39.

## Character 41—Relative Length of Compound

### DESCRIPTION OF CHARACTER

The relative length of the compound bone of the mandible is here defined as the proportion of the compound relative to the total length of the skull. The length of the compound is measured along the dorsal surface of the compound from the posterior dorsal end of the dentary to the posterior end of the compound. The compound has also been called the articular (Guibé, 1970, fig. 92).

### CLASSES AND STATES

The total range of variation in relative length of the compound was segmented by steps of 8.0 per cent, since a span of 8.0 per cent covered most of the intraspecific variation encountered (87.7 per cent—table 125). Eleven classes resulted as shown in Table 126. The mean of each taxon was assigned to a class (table 125).

Four states are recognized:

State I —Classes 3–4 (51.8–67.7 per cent)
State II —Classes 5–7 (67.8–91.7)
State III—Classes 8–11 (91.8–123.7)
State IV—Classes 1–2 (35.8–51.7)

### FAMILIAL RANGES OF VARIATION (Table 127)

Colubridae—This family has States I, II, and IV in a sample from 312 skulls of 194 species of 105 genera. State I occurs in 148 species of 82 genera, II in 25 species of 15 genera, IV in 21 species of 8 genera.

The range in the relative length of the compound is from 35.8 per cent (*Abastor erythrogrammus*) to 88.9 per cent (*Xenodon severus*). The maximum span in a single species is 19.1 per cent (*Natrix*

TABLE 125. Spans in relative length of compound by species and families.

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 204 | 130 | 19 | 15 | 16 | 24 |
| 2 | 1 |  | 1 |  |  |  |
| 7 | 3 | 1 |  |  | 1 | 1 |
| 8 | 1 | 1 |  |  |  |  |
| 9 | 3 | 3 |  |  |  |  |
| 11 | 2 | 2 |  |  |  |  |
| 12 | 1 | 1 |  |  |  |  |
| 13 | 1 | 1 |  |  |  |  |
| 16 | 1 |  |  | 1 |  |  |
| 17 | 2 |  |  | 1 |  | 1 |
| 18 | 2 | 2 |  |  |  |  |
| 19 | 2 | 2 |  |  |  |  |
| 21–30 | 17 | 12 | 2 |  | 2 | 1 |
| 31–40 | 15 | 11 | 1 |  | 3 |  |
| 41–50 | 9 | 3 | 2 | 2 | 1 | 1 |
| 51–60 | 5 | 3 | 1 | 1 |  |  |
| 61–70 | 8 | 5 | 1 | 1 |  | 1 |
| 71–80 | 2 | 1 | 1 |  |  |  |
| 81–90 | 4 | 2 |  | 1 |  | 1 |
| 91–100 | 5 | 3 |  | 1 | 1 |  |

TABLE 125. Spans in relative length of compound by species and families (*continued*).

| Span | All families | Number of Species | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 101–110 | 6 | 2 | | 1 | 1 | 2 |
| 111–120 | 2 | | | | | 2 |
| 121–130 | 6 | 4 | | 1 | | 1 |
| 131–140 | 2 | 1 | | 1 | | |
| 141–150 | 2 | 2 | | | | |
| 160–163 | 2 | 1 | | | 1 | |
| 170–172 | 2 | | 1 | | 1 | |
| 191–195 | 2 | 1 | | 1 | | |
| 206 | 1 | | | | 1 | |
| 233–234 | 2 | | | | 2 | |
| 293 | 1 | | | | 1 | |
| 336 | 1 | | | | | 1 |
| 366 | 1 | | | | 1 | |
| Total | 318 | 194 | 29 | 27 | 32 | 36 |
| Span 8.0% or less | 87.7% | 91.8% | 96.6% | 77.8% | 71.9% | 80.6% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 126. Frequency distribution of species in range classes of relative length of the compound in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 35.8– 43.7 | 1/1 | | | | |
| 2 | 43.8– 51.7 | 20/7 | | | | |
| 3 | 51.8– 59.7 | 80/48 | 5/4 | 10/1 | 1/0 | |
| 4 | 59.8– 67.7 | 68/34 | 6/5 | 7/4 | 1/0 | |
| 5 | 67.8– 75.7 | 21/14 | 9/8 | 7/4 | 7/2 | |
| 6 | 75.8– 83.7 | 3/1 | 7/4 | 0/1 | 11/3 | 7/0 |
| 7 | 83.8– 91.7 | 1/0 | 1/1 | 3/0 | 6/3 | 4/0 |
| 8 | 91.8– 99.7 | | 1/0 | | 5/0 | 13/2 |
| 9 | 99.8–107.7 | | | | | 6/2 |
| 10 | 107.8–115.7 | | | | 1/0 | 4/1 |
| 11 | 115.8–123.7 | | | | | 2/1 |
| Totals | | 194/105 | 29/22 | 27/10 | 32/8 | 36/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 127. Distribution of character states of the relative length of the compound.

| | STATES | | | |
|---|---|---|---|---|
| | IV | I | II | III |
| Classes[1] | 1–2 | 3–4 | 5–7 | 8–11 |
| | | SPECIES | | |
| Colubridae —194 | 10.8% | 76.3% | 12.9% | |
| Elapidae — 29 | | 37.9 | 58.6 | 3.4% |
| Hydrophiidae— 27 | | 63.0 | 37.0 | |
| Viperinae — 32 | | 6.3 | 75.0 | 18.8 |
| Crotalinae — 36 | | | 30.6 | 69.4 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 2 | | | 100.0 | |
| | | GENERA | | |
| Colubridae —105 | 7.6 | 78.1 | 14.3 | |
| Elapidae — 22 | | 40.9 | 59.1 | |
| Hydrophiidae— 10 | | 50.0 | 50.0 | |
| Viperinae — 8 | | | 100.0 | |
| Crotalinae — 6 | | | | 100.0 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 1 | | | 100.0 | |

[1] See Table 126.

*erythrogaster*). However, 91.8 per cent of the species have a span of 8.0 per cent or less.

Elapidae—This family has States I, II, and III in a sample from 43 skulls of 29 species of 22 genera. State I occurs in 11 species of 9 genera, II in 17 species of 13 genera, III in *Dendroaspis viridis*.

The range in the relative length of the compound is from 55.3 per cent (*Cacophis harriettae*) to 91.9 per cent (*Dendroaspis viridis*). The maximum span in a single species is 17.0 per cent (*Ophiophagus hannah*). However, 96.6 per cent of the species have a span of 8.0 per cent or less.

Hydrophiidae—The sea snakes have States I and II in a sample from 64 skulls of 27 species of 10 genera. State I occurs in 17 species and 5 genera, II in 10 species and 5 genera.

The range in the relative length of the compound is from 51.4 per cent (*Hydrophis brookii*) to 96.5 per cent (*Laticauda colubrina*). The maximum span in a single species is 19.5 per cent (*Laticauda colubrina*). However, 77.8 per cent of the species have a span of 8.0 per cent or less.

Viperinae—The true vipers have States I, II, and III in a sample from 76 skulls of 32 species of the 8 genera. State I occurs in two species, II in 24 species and the 8 genera, III in 6 species.

The range in the relative length of the compound is from 54.3 per cent (*Causus lineatus*) to 114.8 per cent (*Bitis arietans*). The maximum span in a single species is 36.6 per cent (*Causus rhombeatus*). However, 71.9 per cent of the species have a span of 8.0 per cent or less.

Crotalinae—The pit vipers have States II and III in a sample from 60 skulls of 36 species of the 6 genera. State II occurs in 11 species, III in 25 species and the 6 genera.

The range in the relative length of the compound is from 76.3 per cent (*Agkistrodon contortrix*) to 133.5 per cent (*Crotalus horridus*). The maximum span in a single species is 33.6 per cent (*Crotalus horridus*). However, 80.6 per cent of the species have a span of 8.0 per cent or less.

*Azemiops* has State I as samples from 2 skulls: range 60.5–62.0 per cent; span 1.6 per cent.

*Atractaspis* only has State II in a sample of 2 skulls from 2 species. The range of variation is 69.6 per cent (*A. dahomeyensis*) to 74.0 per cent (*A. microlepidota*).

### PHYLETICS OF CHARACTER 41

Character State III, the relatively longest compound, does not occur in the colubrids (table 127). The taxa of elapids and viperids having State III are as follows:

- Elapidae
  - *Dendroaspis viridis*
- Viperinae
  - *Bitis arietans*
    - *gabonica*
    - *heraldica*
    - *nasicornis*
  - *Echis coloratus*
  - *Vipera russelii*
- Crotalinae
  - *Agkistrodon acutus*
    - *bilineatus*
    - *rhodostoma*
  - *Bothrops alternatus*
    - *cotiara*
    - *jararacussu*
    - *neuwiedi*
    - *schlegeli*
  - *Crotalus adamanteus*
    - *atrox*
    - *cerastes*
    - *durissus*
    - *horridus*
    - *mitchellii*
    - *molossus*
    - *ruber*
    - *viridis*
  - *Lachesis mutus*
  - *Sistrurus catenatus*
    - *miliarius*
  - *Trimeresurus albolabris*
    - *flavoviridis*
    - *jerdoni*
    - *sumatrana*
    - *wagleri*

We apply the uniqueness criterion (1) to Character State III, for its presence is unique to derived stocks.

Character States II and IV are rare in the colubrids (table 127) (Criterion 2).

State II, a relatively long compound, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Atractus ventrimaculatus*
  - *Boiga blandingi*
  - *Chironius carinatus*
  - *Coluber gemonensis*
    - *hippocrepis*
    - *ventromaculatus*
  - *Cyclagras gigas*
  - *Dasypeltis scabra*
  - *Dimades plicatilis*
  - *Dispholidus typus*
  - *Enhydris plumbea*
  - *Geophis semidoliatus*
  - *Grayia smithi*
  - *Heterodon nasicus*
    - *platyrhinos*
  - *Leptodeira septentrionalis*
  - *Limnophis bicolor*
  - *Natrix taxispilota*
  - *Opisthoplus degener*
  - *Pseustes sulphureus*
  - *Telescopus iterus*
  - *Thamnophis eques*
  - *Tropidodipsas fischeri*
  - *Uromacer catesbyi*
  - *Xenodon severus*
- Elapidae
  - *Acanthophis antarcticus*
  - *Aspidelaps lubricus*
  - *Boulengcrina annulata*
  - *Dendroaspis angusticeps*
  - *Elapsoidea sundevalli*
  - *Leptomicrurus narducci*
  - *Maticora bivirgata*
  - *Micrurus fulvius*
    - sp.
    - *spixi*
  - *Naja naja*
    - *nigricollis*
    - *nivea*
  - *Notechis scutatus*
  - *Ophiophagus hannah*
  - *Pseudechis porphyriacus*
  - *Waltcrinnesia aegyptia*
- Hydrophiidae
  - *Aipysurus duboisii*
    - *foliosquama*
    - *laevis*
  - *Astrotia stokesii*
  - *Emydocephalus annulatus*
  - *Lapemis hardwickii*
  - *Laticauda* (4)
- Viperinae
  - *Adenorhinos barbouri*
  - *Atheris hindii*
    - *hispidus*
    - *squamiger*
    - *superciliaris*
  - *Bitis atropos*
    - *cornuta*
    - *peringueyi*
    - *worthingtoni*
  - *Causus defilippii*
    - *lichtensteini*
    - *rhombeatus*
  - *Cerastes cerastes*
    - *vipera*
  - *Echis carinatus*
  - *Eristicophis macmahoni*
  - *Vipera ammodytes*
    - *aspis*
    - *berus*
    - *latasti*
    - *lebetina*
    - *persica*
    - *ursini*
    - *xanthina*
- Crotalinae
  - *Agkistrodon contortrix*
    - *halys*
    - *hypnale*
    - *nepa*
    - *piscivorus*
  - *Bothrops godmani*
  - *Crotalus lepidus*
  - *Trimeresurus monticola*

| | |
|---|---|
| *mucrosquamatus* | *Atractaspis dahomeyensis* |
| *puniceus* | *microlepidota* |
| *stejnegeri* | |

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total working sample (table 128) (Criterion 3).

TABLE 128. Correlation of States II and IV of Character 41 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 41 | In species having State IV of Character 41 | In total working sample |
| 16 | | 42.9% (7)* | 21.7% (34) |
| 22 | 16.0% (4) | 19.0 (4) | 4.5 (11) |
| 26 | | 23.8 (5) | 12.6 (19) |
| 29 | | 19.0 (4) | 10.1 (27) |
| 33 | 56.0 (13) | | 43.0 (76) |
| 34 | | 15.0 (3) | 6.8 (18) |
| 38 | 28.0 (6) | | 16.2 (27) |
| 40 | 44.0 (10) | | 24.8 (54) |
| 42 | 16.0 (4) | 19.0 (4) | 8.7 (14) |
| 44 | 16.0 (4) | 15.0 (3) | 5.8 (11) |
| 47 | | 76.2 (13) | 48.5 (84) |

* Number of genera.

Also these colubrids have a markedly larger number of species confined to the arboreal and aquatic habitats (56.0 per cent) compared to the relative abundance of arboreal and aquatic colubrid species in the total working sample (31.4 per cent—table 129) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State II is derived (Criterion 8).

TABLE 129. Habitat distribution of colubrid species having States II and IV of Character 41 compared to the total colubrid working sample.

| | Total Working Sample | State II Character 41 | State IV Character 41 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | 28.0 | 42.9 |
| Arboreal | 16.5 | 28.0 | 9.5 |
| Aquatic | 14.9 | 28.0 | 19.0 |
| Subterrestrial | 10.8 | 4.0 | 19.0 |
| Fossorial | 12.4 | 8.0 | 4.8 |
| Variation | 5.3 | 4.0 | 4.8 |
| Unknown | 3.5 | | |

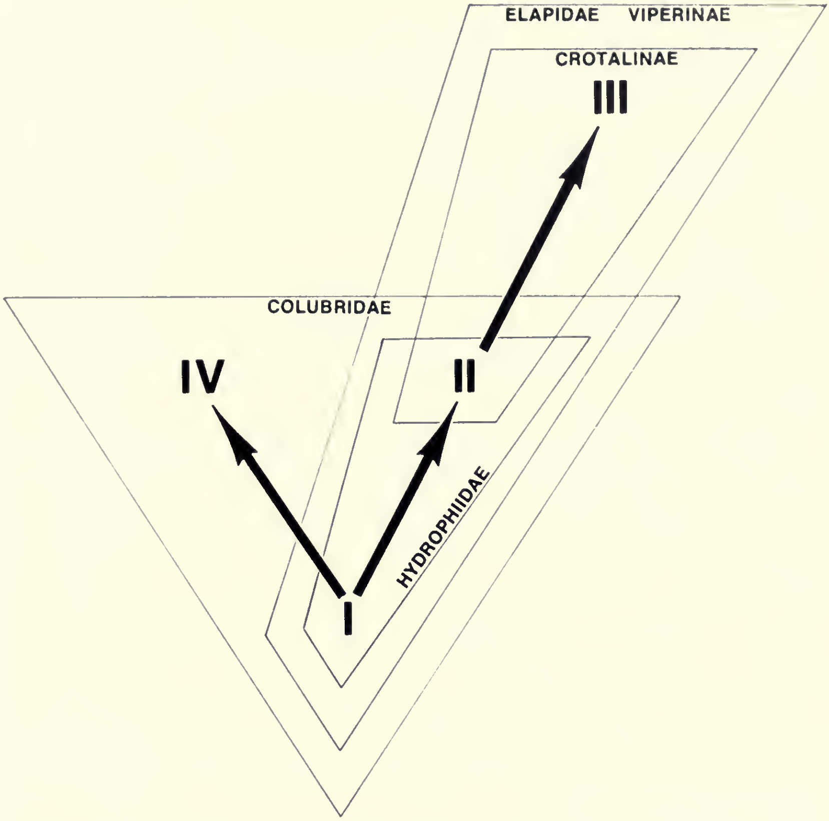

FIG. 40. Distribution among families of states of Character 41. Direction of change among states shown by arrows.

State IV, a relatively short compound, occurs in the following colubrids in our working sample:

Colubridae
  *Abastor erythrogrammus*
  *Achalinus spinalis*
  *Arizona elegans*
  *Boaedon lineatus*
  *Boiga jaspidea*
  *Bothrophthalmus lineatus*
  *Carphophis amoena*
  *Chilomeniscus cinctus*
  *Elaphe dione*
    *flavirufa*
    *radiata*
    *taeniura*
  *Enhydris enhydris*
  *Liopeltis tricolor*
  *Mehelya poensis*
  *Natrix percarinata*
    *valida*
  *Oligodon octolineata*
  *Oxybelis argenteus*
  *Psammodynastes pictus*
  *Thamnophis sauritus*

In these colubrids this character state has a higher frequency of correlation with derived states of eight other characters compared to the frequency distribution of these states of the same eight characters in the total working sample (table 128) (Criterion 3).

Also these colubrids have a larger number of species confined to the subterrestrial habitat (19.0 per cent) compared to the relative abundance of colubrid species in the total working sample (10.8 per cent— table 129) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State IV is derived (Criterion 8).

The nature of this character (i.e., linearly ordered by size—table 126, column 2) makes the arrangement given of the four designated states the most probable.

State IV conforms to this model. It correlates mostly with derived states of different characters (table 128) and it is predominantly abundant in different habitat zones (table 129) than State II.

Our interpretation of the phyletics of Character 41 is shown in Figure 40.

## Character 42—Relative Length of Dentary

### DESCRIPTION OF CHARACTER

The relative length of the dentary bone of the mandible is here defined as the length of the dentary as a proportion of the total length of the skull. The maximum length of the dentary is measured along its dorsal surface.

### CLASSES AND STATES

The total range of variation in relative length of the dentary was segmented by steps of 7.0 per cent, since a span of 7.0 per cent covered most of the intraspecific variation encountered (89.4 per cent—table 130). Ten classes resulted as shown in Table 131. The mean of each taxon was assigned to a class (table 131).

Three states are recognized:

State I —Classes 4–6 (46.8–67.7 per cent)
State II —Classes 1–3 (25.8–46.7)
State III—Classes 7–10 (67.8–95.7)

### FAMILIAL RANGES OF VARIATION (Table 132)

Colubridae—This family has all three states in a sample from 317 skulls of 196 species of 105 genera. State I occurs in 134 species

TABLE 130. Spans in relative length of dentary by species and families.

|  |  | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 207 | 132 | 19 | 15 | 17 | 24 |
| 2 | 1 | 1 |  |  |  |  |
| 6 | 1 | 1 |  |  |  |  |
| 10 | 1 | 1 |  |  |  |  |
| 11 | 3 | 3 |  |  |  |  |
| 12 | 1 | 1 |  |  |  |  |
| 13 | 2 | 1 |  | 1 |  |  |
| 15 | 2 | 1 |  | 1 |  |  |
| 16 | 1 |  |  |  |  | 1 |
| 17 | 1 | 1 |  |  |  |  |
| 18 | 1 |  | 1 |  |  |  |
| 19 | 4 | 2 | 1 |  | 1 |  |
| 21–30 | 16 | 9 | 2 | 1 |  | 4 |
| 31–40 | 14 | 8 | 3 | 2 |  | 1 |
| 41–50 | 11 | 7 | 1 | 1 | 1 | 1 |
| 51–60 | 7 | 5 |  |  | 2 |  |
| 61–70 | 14 | 9 | 1 | 2 | 1 | 1 |
| 71–80 | 9 | 4 | 1 | 2 | 2 |  |
| 81–90 | 3 | 2 |  | 1 |  |  |
| 91–100 | 6 | 3 |  |  | 1 | 2 |
| 101–110 | 3 | 1 |  |  | 2 |  |
| 111–120 | 2 | 1 |  |  | 1 |  |
| 121–130 | 3 |  |  |  | 2 | 1 |
| 131–140 | 4 | 1 |  | 1 | 2 |  |
| 141–150 | 2 |  |  |  | 1 | 1 |
| 159 | 1 | 1 |  |  |  |  |
| 191 | 1 | 1 |  |  |  |  |
| Total | 321 | 196 | 29 | 27 | 33 | 36 |
| Span 7.0% or less | 89.4% | 92.9% | 96.6% | 85.2% | 66.7% | 88.9% |

[1] Excluding *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 131. Frequency distribution of species in range classes of relative length of the dentary in families of advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 25.8–32.7 | 1/1 | 2/2 | 1/1 | | 1/0 |
| 2 | 32.8–39.7 | 5/2 | 7/5 | 4/1 | 1/1 | 5/1 |
| 3 | 39.8–46.7 | 19/14 | 6/4 | 8/1 | 4/0 | 13/2 |
| 4 | 46.8–53.7 | 34/25 | 9/7 | 5/2 | 12/3 | 8/1 |
| 5 | 53.8–60.7 | 46/24 | 4/3 | 8/4 | 9/3 | 5/2 |
| 6 | 60.8–67.7 | 54/27 | 1/1 | 1/1 | 7/1 | 4/0 |
| 7 | 67.8–74.7 | 24/8 | | | | |
| 8 | 74.8–81.7 | 8/2 | | | | |
| 9 | 81.8–88.7 | 3/1 | | | | |
| 10 | 88.8–95.7 | 2/1 | | | | |
| Totals | | 196/105 | 29/22 | 27/10 | 33/8 | 36/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 132. Distribution of character states of the relative length of the dentary.

| | | STATES | |
|---|---|---|---|
| | II | I | III |
| Classes[1] | 1–3 | 4–6 | 7–10 |
| | | SPECIES | |
| Colubridae —196 | 12.8% | 68.4% | 18.9% |
| Elapidae — 29 | 51.7 | 48.3 | |
| Hydrophiidae— 27 | 48.1 | 51.9 | |
| Viperinae — 33 | 15.2 | 84.8 | |
| Crotalinae — 36 | 52.8 | 47.2 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 2 | 50.0 | 50.0 | |
| | | GENERA | |
| Colubridae —105 | 16.2 | 72.4 | 11.4 |
| Elapidae — 22 | 50.0 | 50.0 | |
| Hydrophiidae— 10 | 30.0 | 70.0 | |
| Viperinae — 8 | 12.5 | 87.5 | |
| Crotalinae — 6 | 50.0 | 50.0 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 1 | | 100.0 | |

[1] See Table 131.

and 76 genera, II is 25 species and 17 genera, III in 37 species and 12 genera.

The range in the relative length of the dentary is from 25.8 per cent (*Geophis semidoliatus*) to 97.1 per cent (*Psammodynastes pictus*). The maximum span in a single species is 19.1 per cent (*Natrix cyclopion*). However, 92.9 per cent of the species have a span of 7.0 per cent or less.

Elapidae—This family has States I and II in a sample from 42 skulls of 29 species of 22 genera. State I occurs in 14 species and 11 genera, II in 15 species and 11 genera.

The range in the relative length of the dentary is from 27.5 per cent (*Leptomicrurus narducci*) to 66.4 per cent (*Acanthophis antarcticus*). The maximum span in a single species is 7.2 per cent (*Dendroaspis angusticeps*). However, 96.6 per cent of the species have a span of 7.0 per cent or less.

Hydrophiidae—The sea snakes have States I and II in a sample from 64 skulls of 27 species of 10 genera. State I occurs in 14 species and 7 genera, II in 13 species and 3 genera.

The range in the relative length of the dentary is from 32.3 (*Laticauda colubrina*) to 72.5 per cent (*Pelamis platurus*). The maximum span in a single species is 13.7 per cent (*Pelamis platurus*). However, 85.2 per cent of the species have a span of 7.0 per cent or less.

Viperinae—The true vipers have States I and II in a sample from 73 skulls of 33 species of the 8 genera. State I occurs in 28 species and 7 genera, II in 5 species and one genus.

The range of variation in the relative length of the dentary is from 35.9 per cent (*Adenorhinos barbouri*) to 70.9 per cent (*Cerastes cerastes*). The maximum span in a single species is 14.5 per cent (*Echis carinatus*). However, 66.7 per cent of the species have a span of 7.0 per cent or less.

Crotalinae—The pit vipers have States I and II in a sample from 60 skulls of 36 species of the 6 genera. State I occurs in 17 species and 3 genera, II in 19 species and 3 genera.

The range of variation in the relative length of the dentary is from 30.3 per cent (*Crotalus atrox*) to 69.5 per cent (*Trimeresurus wagleri*). The maximum span in a single species is 14.4 per cent (*Agkistrodon contortrix*). However, 88.9 per cent of the species have a span of 7.0 per cent or less.

*Azemiops* has State I as sampled from 2 skulls: range 50.3 per cent–51.8 per cent; span is 1.6 per cent.

*Atractaspis* has States I and II in a sample from 2 skulls of 2 species. The range of variation is from 45.2 per cent (*A. dahomeyensis*) to 49.6 per cent (*A. microlepidota*).

## Phyletics of Character 42

Character States II and III are relatively rare in the colubrids (table 132) (Criterion 2).

State II, a relatively short dentary, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Achalinus spinalis*
- *Aparallactus lunulatus*
  - *werneri*
- *Atractus elaps*
  - *ventrimaculatus*
- *Calamaria septentrionalis*
- *Calamelaps unicolor*
- *Carphophis amoena*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Chilorhinophis carpenteri*
- *Conopsis lineatus*
  - *nasus*
- *Geophis semidoliatus*
- *Haldea striatula*
- *Lycodon striatus*
- *Lytorhynchus diadema*
  - *maynardi*
- *Oligodon octolineata*
- *Phyllorhynchus decurtatus*

- *Sonora episcopa*
- *Stenorhina degenhardti*
- *Stilostoma extenuatum*
- *Tantilla gracilis*
- *Tropidodipsas fischeri*

Elapidae
- *Aspidelaps lubricus*
- *Brachyurophis semifasciata*
- *Dendroaspis angusticeps*
  - *viridis*
- *Elaps lacteus*
- *Elapsoidea sundevalli*
- *Leptomicrurus collaris*
  - *narducci*
- *Maticora bivirgata*
- *Micrurus fulvius*
  - sp.
  - *spixi*
- *Rhynchoelaps bertholdi*
- *Vermicella annulata*
- *Walterinnesia aegyptia*

Hydrophiidae
- *Aipysurus apraefrontalis*
  - *duboisii*
  - *foliosquama*
  - *fuscus*
- *Emydocephalus annulatus*
- *Hydrophis brookii*
  - *fasciatus*
  - *klossi*
- *Laticauda* (4)
- *Microcephalophis cantoris*

Viperinae
- *Adenorhinos barbouri*
- *Causus lichtensteini*
  - *lineatus*
- *Vipera berus*
  - *ursinii*

Crotalinae
- *Agkistrodon halys*
- *Bothrops alternatus*
  - *cotiara*
  - *godmani*
  - *neuwiedi*
- *Crotalus* (10)
- *Lachesis mutus*
- *Sistrurus* (2)
- *Trimeresurus jerdoni*

*Atractaspis dahomeyensis*

In these colubrids this character state has a higher frequency of correlation with derived states of 16 other characters compared to the frequency distribution of these states of the same 16 characters in the total working sample (table 133) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the subterrestrial and fossorial habitat (28.8 per cent, 64.0 per cent) compared to the relative abundance of subterrestrial and fossorial colubrid species in the total sample (10.8 per cent, 12.4 per cent—table 134) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State II is derived (Criterion 8).

State III, a relatively long dentary, occurs in the following colubrids in our working sample:

Colubridae
- *Abastor erythrogrammus*
- *Boaedon lineatus*
- *Boiga blandingi*
  - *cynodon*
  - *dendrophila*
- *Bothrophthalmus lineatus*
- *Chironius fuscus*
- *Cyclagras gigas*
- *Dimades plicatilis*
- *Elaphe flavirufa*
  - *obsoleta*
  - *taeniura*

*Enhydris chinensis*
*enhydris*
*Farancia abacura*
*Grayia smithi*
*Leptodeira annulata*
*Malpolon monspessulanus*
*Natrix aequifasciata*
*cyclopion*
*erythrogaster*
*natrix*
*percarinata*
*rhombifera*
*rigida*
*sipedon*
*taxispilota*
*tessellata*
*valida*
*Psammodynastes pictus*
*pulverulentus*
*Pseustes poecilonotus*
*Thamnophis eques*
*macrostemma*
*sirtalis*
*Xenodon merremii*
*severus*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total working sample (table 133) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the aquatic habitat (43.2 per cent) compared to the rela-

TABLE 133. Correlation of States II and III of Character 42 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 42 | In species having State III of Character 42 | In total working sample |
| 1 | 24.0% (5)* | | 14.3% (28) |
| 5 | 20.0 (4) | | 3.5 (9) |
| 7 | 76.0 (15) | | 25.5 (56) |
| 9 | 16.0 (4) | | 6.8 (14) |
| 14 | 16.0 (3) | | 3.5 (7) |
| 16 | | 45.9% (8) | 21.7 (34) |
| 17 | | 54.1 (6) | 35.4 (48) |
| 19 | 75.0 (15) | | 36.8 (68) |
| 22 | 52.0 (10) | | 4.5 (11) |
| 28 | 40.0 (7) | | 11.7 (26) |
| 29 | 54.5 (11) | | 10.1 (27) |
| 31 | | 29.7 (8) | 19.5 (44) |
| 32 | 63.6 (10) | | 26.3 (55) |
| 34 | 31.8 (7) | | 6.8 (18) |
| 36 | 29.2 (7) | | 6.1 (16) |
| 37 | | 51.4 (12) | 22.9 (54) |
| 39 | | 27.0 (6) | 9.0 (19) |
| 40 | 56.0 (12) | | 24.8 (54) |
| 41 | 30.4 (7) | 45.9 (14) | 10.9 (20) |
| 48 | 16.7 (3) | | 6.2 (11) |
| 49 | 29.2 (15) | | 15.5 (26) |

* Number of genera.

TABLE 134. Habitat distribution of colubrid species having States II and III of Character 42 compared to the total colubrid working sample.

| | Total Working Sample | State II Character 42 | State III Character 42 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | 8.0 | 27.0 |
| Arboreal | 16.5 | | 13.5 |
| Aquatic | 14.9 | | 43.2 |
| Subterrestrial | 10.8 | 28.8 | 5.4 |
| Fossorial | 12.4 | 64.0 | |
| Variation | 5.3 | | 10.8 |
| Unknown | 3.5 | | |

tive abundance of aquatic colubrid species in the total working sample (14.9 per cent—table 134) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

State II probably arose in a different sequential direction than State III because II correlates mostly with derived states of different characters (table 133) and is predominantly abundant in different habitat zones (table 134).

The serial nature of this character (i.e., numerical order—table 131, column 2) makes the arrangement given of the three designated states the most probable.

Our interpretation of the phyletics of Character 42 is shown in Figure 24.

## Character 43—Presence of the Splenial and Angular

### DESCRIPTION OF CHARACTER

There are usually two small bones situated on the medial surface of the mandible and wedged between the dentary and compound. The anterior bone is the splenial and the posterior bone is the angular. The angular also has been called the complementary (Radovanovic, 1937). Occasionally a single bone is present (see below). The splenial is usually considered to be the bone in the process of disappearing (Romer, 1956, p. 203). We do not know if one of these bones is lost and replaced by the other or whether fusion of these two elements occurs. Therefore, we are using the presence of a pair of bones or the presence of a single bone in this site as distinct states of this character without assessing which bone(s) remains intact. We (Marx and Rabb, 1965, fig. 34) had previously made a judgment as to which bone remains from its positional relationships but here record our strong reservation about this evaluation. We suspect disappearance and fusion both occur. There are specimens with these two bones in partial fusion. Also when a single bone is present it appears in various sizes and shapes, suggesting fusion with the other.

Three states are recognized:

State I —two bones
State II —one bone
State III—intraspecific variation, both States I and II present

### Familial Ranges of Variation (Table 135)

Colubridae—This family has all three states in a sample of 308 species of 163 genera (581 skulls). State I occurs in 302 species of 160 genera (566 skulls), II in 4 species of 3 genera (10 skulls), III in 2 species of 2 genera (5 skulls).

Intrageneric variation occurs in *Mehelya* (II and III) and *Lycodon* (I and III).

Elapidae, Hydrophiidae—The elapids and sea snakes only have State I in a sample of 110 species (68, 42 respectively) of 53 genera (37: 16) (253: 110, 143 skulls).

TABLE 135. Distribution of character states of the presence of the splenial and angular.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | |
| Description | Two bones Present | One bone Present | Intraspecific Variation | |
| | SPECIES[1] | | | |
| Colubridae —308 | 98.1% | 1.3% | 0.6% | |
| Elapidae — 68 | 100.0 | | | |
| Hydrophiidae— 42 | 100.0 | | | |
| Viperinae — 34 | 44.1 | 50.0 | 5.9 | |
| Crotalinae — 45 | 64.4 | 31.1 | 4.4 | |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 5 | 100.0 | | | |
| | GENERA | | | INTRAGENERIC VARIATION |
| Colubridae —163 | 97.5 | 1.2 | | 1.2% |
| Elapidae — 37 | 100.0 | | | |
| Hydrophiidae— 16 | 100.0 | | | |
| Viperinae — 8 | 25.0 | 50.0 | | 25.0 |
| Crotalinae — 6 | 16.7 | | | 83.3 |
| *Azemiops* — 1 | 100.0 | | | |
| *Atractaspis* — 1 | 100.0 | | | |

[1] Working sample.

Viperinae—The true vipers have all three states in a sample of 34 species of the 8 genera (95 skulls). State I occurs in 15 species of 4 genera (31 skulls), II in 17 species of 4 genera (52 skulls), III in 2 species of 2 genera (12 skulls).

Intrageneric variation occurs in *Causus* and *Echis* (I and III).

Crotalinae—The pit vipers have all three states in a sample of 45 species of the 6 genera (82 skulls). State I occurs in 29 species of 5 genera (56 skulls), II in 14 species of 4 genera (19 skulls), III in the 2 species of *Sistrurus* (7 skulls).

Intrageneric variation occurs in five genera.

*Azemiops* has State I (2 skulls).

*Atractaspis* has State I in a sample of 5 species (8 skulls).

### PHYLETICS OF CHARACTER 43

Character State II is rare in the colubrids (table 135) (Criterion 2).

State II, a single bone, occurs in the following colubrids (plus other taxa):

Colubridae
- *Grayia smithi*
- *Lycophidion capense*
- *Mehelya chanleri*
  - *poensis*

Viperinae
- *Adenorhinos*
- *Atheris*
- *Bitis*
- *Cerastes*

Crotalinae
- *Agkistrodon hypnale*
  - *nepa*
  - *rhodostoma*
- *Bothrops dunni*
  - *lansbergii*
- *Crotalus basiliscus*
  - *durissus*
  - *molossus*
- *Trimeresurus albolabris*
  - *mucrosquamatus*
  - *okinavensis*
  - *puniceus*
  - *stejnegeri*
  - *sumatranus*

The colubrids are all from tropical Africa (Criterion 6). Bogert (1940, p. 11) considered *Grayia* unrelated to *Lycophidion* and *Mehelya* and the latter two closely related. Underwood (1967) put these genera in Lycodontinae of Dipsadidae and *Grayia* in Natricidae. There is agreement as to the lack of relationships of *Grayia* to the other stock and an agreement as to the close relationship of the other genera. This state otherwise appears only in the Viperidae (Criterion 7). In the Viperinae this state is almost exclusively restricted to the tropical African true vipers (15 of 17 species).

In these true vipers it appears that parallelism occurred in the reduction to one bone for the loss occurs in all three major generic groupings, the primitive *Causus*, the intermediate Palearctic vipers and the Ethiopian vipers. If this direction of change is also true for the ancestral colubrids, it occurred at least twice in the two divergent stocks of colubrids having a single bone (see above).

The application of three criteria (2, 6, 7) suggests that this state is derived (Criterion 8).

State III occurs in the following colubrids (plus other taxa):

Colubridae
  *Lycodon aulicus*
  *Mehelya capensis*
Viperinae
  *Causus rhombeatus*
  *Echis carinatus*
Crotalinae
  *Sistrurus*

State III is an intermediate sequential state because each taxon with this state has both States I and II.

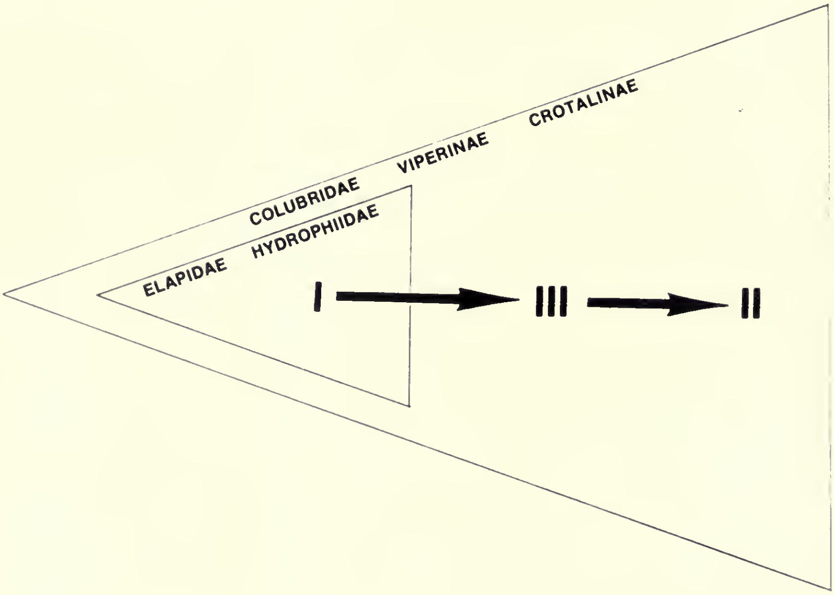

FIG. 41. Distribution among families of states of Character 43. Direction of change among states shown by arrows.

Our interpretation of the phyletics of Character 43 is shown in Figure 41.

## Character 44—Number of Maxillary Teeth

### DESCRIPTION OF CHARACTER

The maxillaries are dentigerous bones located on the outer edge of the anterior roof of the mouth. The number of teeth (or tooth sockets) on the maxillary bones was counted. Each bone was recorded separately.

### CLASSES AND STATES

The total range of variation in number of maxillary teeth was segmented by steps of four, since a span of four covers most of the intraspecific variation encountered (95.2 per cent—table 136). Ten classes resulted as shown in Table 137. The mean of each taxon was assigned to a class (table 137).

Three states are recognized:

State I —Classes 3–7 (7.5–27.49)
State II —Classes 1–2 (0–7.49)
State III—Classes 8–10 (27.5–39.49)

### FAMILIAL RANGES OF VARIATION (Table 138)

Colubridae—This family has all three states in a sample of 782 maxillary bones from 406 skulls of 219 species of 112 genera. State I occurs in 199 species and 96 genera, II in 9 species and 9 genera, III in 11 species and 7 genera.

The range in the number of maxillary teeth is from 2 (*Opisthoplus degener*) to 36 (*Chironius fuscus, Opisthotropis kuatunensis*). The maximum span in a single species is 8 (*Opisthotropis kuatunensis*). However, 92.6 per cent of the species have a span of 4 or less (table 136). The maximum span in a single specimen is 6 (*Boaedon lineatus*—FMNH 51684).

Elapidae—This family has States I and II in a sample of 282 maxillary bones from 147 skulls of 54 species of 37 genera. State I occurs in 6 species of 4 genera, II in 48 species of 33 genera.

The range in the number of maxillary teeth is from 1 (13 species of 8 genera) to 13 (3 species of *Demansia*). The maximum span in a species is 5 (*Demansia textilis*). However 98.1 per cent of the species

TABLE 136. Spans in number of maxillary teeth by species and families.

| | | Number of Species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae | Elapidae[1] | Hydrophiidae | Viperinae[2] | Crotalinae |
| 1 | 227 | 95 | 38 | 16 | 33 | 45 |
| 2 | 88 | 63 | 10 | 15 | | |
| 3 | 45 | 33 | 4 | 8 | | |
| 4 | 13 | 12 | 1 | | | |
| 5 | 11 | 8 | 1 | 2 | | |
| 6 | 2 | 2 | | | | |
| 7 | 5 | 5 | | | | |
| 8 | 1 | 1 | | | | |
| Totals | 392 | 219 | 54 | 41 | 33 | 45 |
| Span 4 or less | 95.2% | 92.6% | 98.1% | 95.1% | 100.0% | 100.0% |

[1] Including part of Bogert, 1943, Table 1.

[2] Excluding *Azemiops* and *Atractaspis*.

TABLE 137. Frequency distribution of species in range classes of number of maxillary teeth in families of advanced snakes.

| Classes | Range | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 0 – 3.49 | 2/2 | 25/15 | 5/1 | 33/8 | 45/6 |
| 2 | 3.50– 7.49 | 7/7 | 23/18 | 16/7 | | |
| 3 | 7.50–11.49 | 32/15 | 4/4 | 15/7 | | |
| 4 | 11.50–15.49 | 64/39 | 2/0 | 4/1 | | |
| 5 | 15.50–19.49 | 49/23 | | 1/0 | | |
| 6 | 19.50–23.49 | 30/10 | | | | |
| 7 | 23.50–27.49 | 24/9 | | | | |
| 8 | 27.50–31.49 | 6/4 | | | | |
| 9 | 31.50–35.49 | 4/3 | | | | |
| 10 | 35.50–39.49 | 1/0 | | | | |
| Totals | 392/179 | 219/112 | 54/37 | 41/16 | 33/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 138. Distribution of character states of the number of maxillary teeth.

| | | STATES | |
|---|---|---|---|
| | I | II | III |
| Classes[1] | 3–7 | 1–2 | 8–10 |
| | | SPECIES | |
| Colubridae —219 | 90.9% | 4.1% | 5.0% |
| Elapidae — 54 | 11.1 | 88.9 | |
| Hydrophiidae— 41 | 48.8 | 51.2 | |
| Viperinae — 33 | | 100.0 | |
| Crotalinae — 45 | | 100.0 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 5 | | 100.0 | |
| | | GENERA | |
| Colubridae —112 | 85.7 | 8.0 | 6.3 |
| Elapidae — 37 | 10.8 | 89.2 | |
| Hydrophiidae— 16 | 50.0 | 50.0 | |
| Viperinae — 8 | | 100.0 | |
| Crotalinae — 6 | | 100.0 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 1 | | 100.0 | |

[1] See Table 137.

have a span of 4 or less (table 136). The maximum span in a single specimen is 4 (*Demansia olivacea*—AMNH 82478).

Hydrophiidae—The sea snakes have States I and II in a sample of 236 maxillary bones from 122 skulls of 41 species of the 16 genera. State I occurs in 20 species of 8 genera, II in 21 species of 8 genera.

The range in the number of maxillary teeth is from 2 (two species of *Emydocephalus*) to 16 (*Aipysurus eydouxi, Hydrophis caerulescens*). The maximum span in a single species is 5 (*Hydrophis cyanocinctus, Pelamis platurus*). However 95.1 per cent of the species have a span of 4 or less (table 136). The maximum span in a single specimen is 3 (6 species of 4 genera).

Viperinae, Crotalinae, *Azemiops, Atractaspis*—All specimens of these four taxa have a single functional tooth on the maxilla (State II). The sample is from 398 maxillary bones (210, 168, 4, 16 respectively) of 199 skulls (105, 84, 2, 8) of 84 species (33, 45, 1, 5) of 16 genera (8, 6, 1, 1).

## PHYLETICS OF CHARACTER 44

Character States II and III are rare in the colubrids (table 138) (Criterion 2).

State II, small number of maxillary teeth, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Aparallactus lunulatus*
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Dasypeltis scabra*
  - *Dispholidus typus*
  - *Lystrophis d'orbignyi*
  - *Miodon gabonensis*
  - *Opisthoplus degener**
  - *Tomodon dorsatus**
- Elapidae
  - *Acanthophis antarcticus*
  - *Apistocalamus lonnbergi*
    - *loriae*
  - *Aspidelaps lubricus*
  - *Boulengerina annulata*
  - *Brachyaspis curta*
  - *Brachyurophis semifasciata*
  - *Bungarus fasciatus*
    - *multicinctus*
  - *Calliophis japonicus*
  - *Dendroaspis angusticeps*
    - *jamesoni*
    - *viridis*
  - *Denisonia coronoides*
  - *Elapognathus minor*
  - *Elaps lacteus*
  - *Elapsoidea sundevalli*
  - *Furina diadema*
  - *Hemachatus haemachatus*
  - *Hoplocephalus bitorquatus*
  - *Leptomicrurus collaris*
    - *narducci*
  - *Maticora bivirgata*
  - *Micropechis elapsoides*
    - *ikaheka*
  - *Micruroides euryxanthus*
  - *Micrurus fulvius*
    - sp.
    - *spixi*
  - *Naja haje*
    - *melanoleuca*
    - *naja*
    - *nigricollis*
    - *nivea*
  - *Notechis scutatus*
  - *Ogmodon vitianus*
  - *Ophiophagus hannah*
  - *Parapistocalamus hedigeri*
  - *Pseudechis australis*
    - *papuanus*
    - *porphyriacus*
  - *Pseudohaje goldii*
    - *nigra*
  - *Rhynchoelaps bertholdi*
  - *Toxicocalamus stanleyanus*
  - *Ultrocalamus preussi*
  - *Vermicella annulata*
  - *Walterinnesia aegyptia*
- Hydrophiidae
  - *Aipysurus apraefrontalis*
    - *foliosquama*
  - *Emydocephalus annulatus*
    - *ijimae*
  - *Enhydrina schistosa*
  - *Hydrelaps darwiniensis*
  - *Hydrophis brookii*
    - *fasciatus*
    - *kingi*
    - *klossi*
    - *melanosoma*
  - *Lapemis curtus*
    - *hardwickii*
  - *Laticauda colubrina*
    - *laticaudata*
    - *schistorhynchus*
    - *semifasciata*
  - *Microcephalophis cantoris*
    - *gracilis*
  - *Thalassophina viperina*
  - *Thalassophis anomalus*
- Viperinae (all taxa)
- Crotalinae (all taxa)
- *Azemiops*
- *Atractaspis* (all taxa)

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* *Opisthoplus* and *Tomodon* are suspected of being congeneric by Bailey (1967, p. 160).

TABLE 139. Correlation of States II and III of Character 44 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State II of Character 44 | In species having State III of Character 44 | In total working sample |
| 1 | 77.8% (7)* | | 25.5% (56) |
| 11 | | 54.5% (5) | 26.7 (50) |
| 13 | 55.6 (5) | 54.5 (5) | 31.8 (54) |
| 17 | | 63.6 (5) | 35.4 (48) |
| 22 | 33.3 (3) | | 4.5 (11) |
| 29 | 66.7 (6) | | 10.1 (27) |
| 31 | 62.5 (5) | | 19.5 (44) |
| 32 | 66.7 (6) | | 26.3 (55) |
| 34 | 37.5 (3) | | 6.8 (18) |
| 35 | 33.3 (3) | | 2.0 (6) |
| 36 | 33.3 (3) | | 6.1 (16) |
| 39 | 33.3 (3) | | 9.0 (15) |
| 40 | 44.4 (4) | | 24.8 (54) |
| 42 | 42.9 (3) | | 8.7 (14) |
| 46 | 77.8 (7) | | 26.9 (52) |
| 47 | | 72.7 (7) | 48.5 (84) |
| 49 | 50.0 (26) | 54.5 (5) | 15.5 (26) |
| 50 | 50.0 (24) | 90.9 (8) | 20.0 (24) |

* Number of genera.

In these colubrids this character state has a higher frequency of correlation with derived states of 15 other characters compared to the frequency distribution of these states of the same 15 characters in the total sample (table 139) (Criterion 3).

The striking similarity of the above colubrids and other taxa is that all but two of these species are venomous, either rear or front-fanged. We conclude that with the development of the poison-injecting apparatus there is also a strong selection for reduction in numbers of maxillary teeth.

TABLE 140. Habitat distribution of colubrid species having States II and III of Character 44 compared to the total colubrid working sample.

| | Total Working Sample | STATES | |
|---|---|---|---|
| | | II | III |
| Terrestrial | 36.2% | 11.1% | 36.4% |
| Arboreal | 16.5 | 44.4 | |
| Aquatic | 14.9 | | 36.4 |
| Subterrestrial | 10.8 | | |
| Fossorial | 12.4 | 44.4 | |
| Variation | 5.3 | | 27.3 |
| Unknown | 3.5 | | |

Also these colubrids have a markedly larger number of species confined to the arboreal and fossorial habitats (88.8 per cent) compared to the relative abundance of arboreal and fossorial colubrid species in the total sample (28.9 per cent—table 140) (Criterion 5).

In addition, the geographic range of these colubrids is restricted to tropical Africa or South America (Criterion 6).

The application of four criteria (2, 3, 5, 6) strongly indicates that State II is derived (Criterion 8).

State III, large number of maxillary teeth, occurs only in the following colubrids in our working sample:

Colubridae
- *Chironius carinatus*
  - *fuscus*
- *Dromicodryas bernieri*
- *Drymobius bifossatus*
- *Liopeltis tricolor*
- *Liopholidophis lateralis*
- *Mehelya poensis*
- *Natrix percarinata*
  - *trianguligera*
- *Opisthotropis kuatunensis*
- *Philothalmus irregularis*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 139) (Criterion 3).

All these species lack fangs. These colubrids have a proportionately larger number of species confined to the aquatic habitat (36.4 per cent) compared to the relative abundance of aquatic colubrid species in the total sample (14.9 per cent—table 140) (Criterion 5). Large numbers of maxillary teeth are presumably of special importance in grabbing and engulfing certain kinds of prey, whereas few maxillary teeth (State II) are associated with puncturing and poisoning of prey with fangs, the dentition of other bones being used in engulfing prey.

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

State II probably arose in a different sequential direction from State III for they correlate mostly with derived states of different characters (table 139), are predominantly abundant in taxa from different habitat zones (table 140), and probably represent different functions (Criterion 4).

The serial nature of this character (i.e., numerical order—table 137, column 2) makes the arrangement given of the three designated states the most probable.

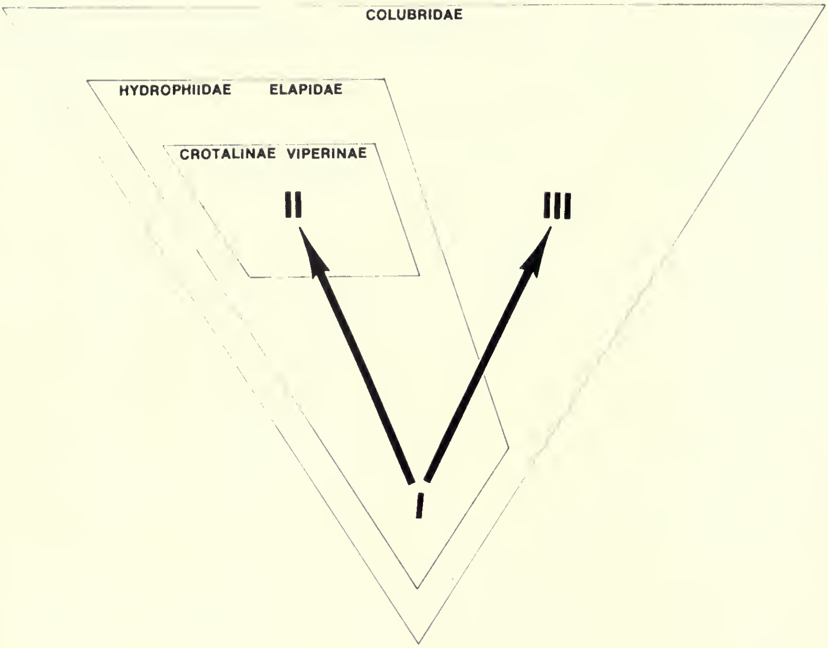

Fig. 42. Distribution among families of states of Character 44. Direction of change among states shown by arrows.

Our interpretation of the phyletics of Character 44 is shown in Figure 42.

## Character 45—Relative Length of Longest Maxillary Tooth

### Description of Character

The relative length of the longest maxillary tooth is here defined as the length of the tooth as a proportion of the total length of the skull.

### Classes and States

The total range of variation in relative length of longest maxillary tooth was segmented by steps of 7.0 per cent since a span of 7.0 per cent covered most of the intraspecific variation encountered (96.8 per cent—table 141). Eight classes resulted as shown in Table 142. The mean of each taxon was assigned to a class (table 142).

Four states are recognized:

State I —Classes 1–2 (0.3–13.2 per cent)

TABLE 141. Spans in relative length of fangs by species and families.

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1[2] | 188 | 112 | 25 | 13 | 13 | 26 |
| 2 | 1 |  |  | 1 |  |  |
| 5 | 1 |  |  |  | 1 |  |
| 12 | 1 | 1 |  |  |  |  |
| 15 | 1 |  |  |  |  | 1 |
| 21–30 | 5 |  |  |  | 5 |  |
| 31–40 | 5 |  |  |  | 3 | 2 |
| 41–50 | 3 |  |  |  | 2 | 1 |
| 51–60 | 3 |  |  |  | 2 | 1 |
| 61–70 | 4 |  |  |  | 1 | 3 |
| 98 | 1 |  |  |  |  | 1 |
| 99 | 1 |  |  |  | 1 |  |
| 109 | 1 |  |  |  |  | 1 |
| 112 | 1 |  |  |  |  | 1 |
| 139 | 2 |  |  |  | 2 |  |
| 177 | 1 |  |  |  | 1 |  |
| Total | 219 | 113 | 25 | 14 | 31 | 37 |
| Span 7.0% or less | 96.8% | 100.0% | 100.0% | 100.0% | 87.1% | 91.9% |

[1] Excludes *Azemiops* and *Atractaspis*.

[2] 0.1%

TABLE 142. Frequency distribution of species in range classes of relative length of teeth in advanced snakes.

| Classes | Range (%) | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 0.3– 7.2 | 43/43 | 1/1 | 1/1 | | |
| 2 | 7.3–13.2 | 48/47 | 12/11 | 12/4 | | |
| 3 | 13.3–20.2 | 20/19 | 10/8 | 1/0 | 7/2 | |
| 4 | 20.3–27.2 | 2/2 | 2/2 | | 4/1 | 4/1 |
| 5 | 27.3–34.2 | | | | 10/3 | 10/1 |
| 6 | 34.3–41.2 | | | | 7/1 | 12/3 |
| 7 | 41.3–48.2 | | | | 2/1 | 9/1 |
| 8 | 48.3–55.2 | | | | 1/0 | 2/0 |
| Totals | | 113/111 | 25/22 | 14/5 | 31/8 | 37/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

State II —Classes 3–4 (13.3–27.2)
State III—Classes 5–6 (27.3–41.2)
State IV—Classes 7–8 (41.3–55.2)

### Familial Ranges of Variation (Table 143)

Colubridae—This family has States I and II in a sample from 114 skulls of 113 species of 111 genera. State I occurs in 91 species of 90 genera, II in 22 species of 21 genera.

TABLE 143. Distribution of character states of the relative length of the longest maxillary tooth.

| | STATES | | | |
|---|---|---|---|---|
| | I | II | III | IV |
| Classes[1] | 1–2 | 3–4 | 5–6 | 7–8 |
| | SPECIES | | | |
| Colubridae —113 | 80.4% | 19.7% | | |
| Elapidae — 25 | 52.0 | 48.0 | | |
| Hydrophiidae— 14 | 92.8 | 7.1 | | |
| Viperinae — 31 | | 35.5 | 54.8% | 9.7% |
| Crotalinae — 37 | | 10.8 | 59.5 | 29.7 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 4 | | | 100.0 | |
| | GENERA | | | |
| Colubridae —111 | 80.9 | 19.1 | | |
| Elapidae — 22 | 54.5 | 45.5 | | |
| Hydrophiidae— 5 | 100.0 | | | |
| Viperinae — 8 | | 37.5 | 50.0 | 12.5 |
| Crotalinae — 6 | | 16.7 | 66.7 | 16.7 |
| *Azemiops* — 1 | | 100.0 | | |
| *Atractaspis* — 1 | | | 100.0 | |

[1] See Table 142.

The range of variation in the relative length of the longest maxillary tooth is from 0.4 per cent (*Alsophis sanctae-crucis*) to 22.2 per cent (*Xenodon colubrinus*). The maximum span in a single species is 1.2 per cent (*Natrix cyclopion*).

Elapidae—This family has States I and II in a sample from 25 skulls of 25 species of 22 genera. State I occurs in 13 species of 12 genera, II in 12 species of 10 genera.

The range of variation in the relative length of the longest maxillary tooth is from 7.2 per cent (*Hoplocephalus bitorquatus*) to 25.7 per cent (*Acanthophis antarcticus*).

Hydrophiidae—The sea snakes have States I and II in a sample from 15 skulls of 14 species of 5 genera. State I occurs in 13 species and 5 genera, II in *Laticauda semifasciata.*

The range of variation in the relative length of the longest maxillary tooth is from 4.1 per cent (*Pelamis platurus*) to 14.7 per cent (*Laticauda semifasciata*). The maximum span in a single species is 0.2 per cent (*Hydrophis klossi*).

Viperinae—The true vipers have States II, III, and IV in a sample from 80 skulls of 31 species of the 8 genera. State II occurs in 11 species and 3 genera, III in 17 species and 4 genera, IV in 3 species and 1 genus.

The range of variation in the relative length of the longest maxillary tooth is from 13.3 per cent (*Adenorhinos barbouri, Vipera berus*) to 60.3 per cent (*Bitis gabonica*). The maximum span in a single species is 17.7 per cent (*B. gabonica*). However 87.1 per cent of the species have a span of 7.0 per cent or less.

Crotalinae—The pit vipers have States II, III, and IV in a sample from 60 skulls of 37 species of the 6 genera. State II occurs in 4 species and 1 genus, III in 22 species and 4 genera, IV in 11 species and 1 genus.

The range of variation in the relative length of the longest maxillary tooth is from 16.3 per cent (*Crotalus lepidus*) to 51.4 per cent (*Crotalus adamanteus*). The maximum span is 11.2 per cent (*Trimeresurus stejnegeri*). However 91.9 per cent of the species have a span of 7.0 per cent or less.

*Azemiops* has State II from a sample of 2 skulls: range is 21.6 per cent to 21.9 per cent; span of 0.4 per cent.

*Atractaspis* has State III as sampled from 7 skulls of 4 species. The range of variation in the relative length of the longest maxillary tooth is from 27.7 per cent (*A. irregularis*) to 32.6 per cent (*A. bibroni*). The maximum span is 2.3 per cent (*A. irregularis*).

### Phyletics of Character 45

As Klauber (1939, p. 51) has demonstrated for *Crotalus* species, ". . . it is in general true that larger species have proportionally longer fangs than smaller species." We therefore plotted the actual fang length against the total skull length of each specimen in all taxa of "vipers" (figs. 43–44). There is an isometric progression, for the longer the skull (larger species) the longer the fangs. This confirms Klauber's conclusions for *Crotalus* and applies to the entire family

Viperidae. However, there is an allometric progression for the relative longest maxillary tooth length in Colubridae, Elapidae, and Hydrophiidae (figs. 45–46).

Character States III and IV, relatively longest maxillary tooth, do not occur in the colubrids (table 143) unless *Atractaspis* is considered. The taxa having State III in our working sample are:

- Viperinae
  - *Atheris hindii*
    - *hispidus*
    - *nitschei*
    - *squamiger*
    - *superciliaris*
  - *Bitis atropos*
    - *cornuta*
    - *heraldica*
    - *worthingtoni*
  - *Cerastes cerastes*
    - *vipera*
  - *Echis carinatus*
    - *coloratus*
  - *Vipera ammodytes*
    - *persica*
    - *russelii*
    - *xanthina*
- Crotalinae
  - *Agkistrodon bilineatus*
    - *contortrix*
    - *hypnale*
    - *nepa*
    - *piscivorus*
  - *Bothrops cotiara*
    - *neuwiedi*
    - *schlegeli*
  - *Crotalus cerastes*
    - *horridus*
    - *mitchellii*
    - *pusillus*
    - *ruber*
    - *viridis*
  - *Sistrurus miliarius*
  - *Trimeresurus albolabris*
    - *flavoviridis*
    - *jerdoni*
    - *monticola*
    - *puniceus*
    - *stejnegeri*
    - *wagleri*
- *Atractaspis bibroni*
  - *dahomeyensis*
  - *irregularis*
  - *microlepidota*

The taxa having State IV in our working sample are:

- Viperinae
  - *Bitis arietans*
    - *gabonica*
    - *nasicornis*
- Crotalinae
  - *Agkistrodon acutus*
    - *rhodostoma*
  - *Bothrops alternatus*
    - *jararacussu*
  - *Crotalus adamanteus*
    - *atrox*
    - *durissus*
    - *molossus*
  - *Lachesis mutus*
  - *Trimeresurus mucrosquamatus*
    - *sumatranus*

We apply the uniqueness criterion (1) to Character States III and IV, for their presence is unique to derived stocks.

State II, a relatively long maxillary tooth, occurs in the following colubrids (plus other taxa) in our working sample:

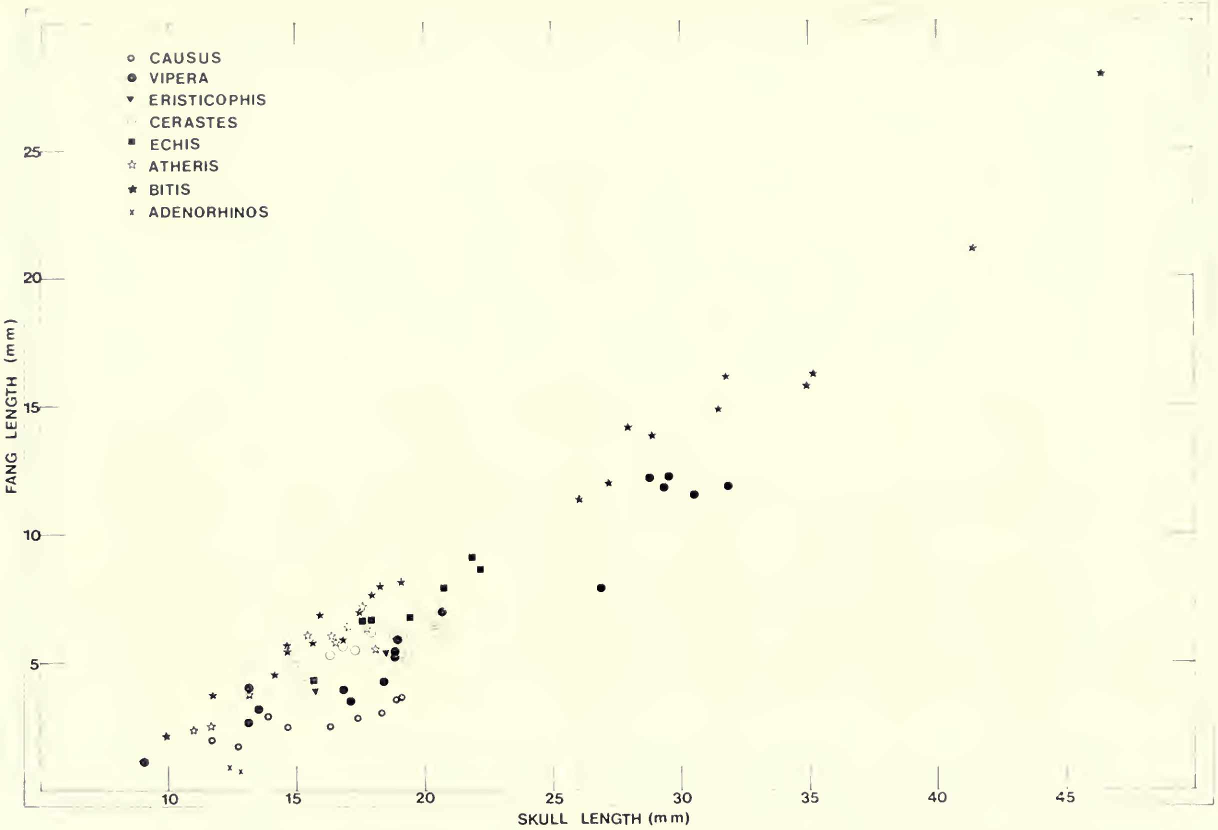

FIG. 43. Relation between longest maxillary tooth length and skull length in specimens of Viperinae

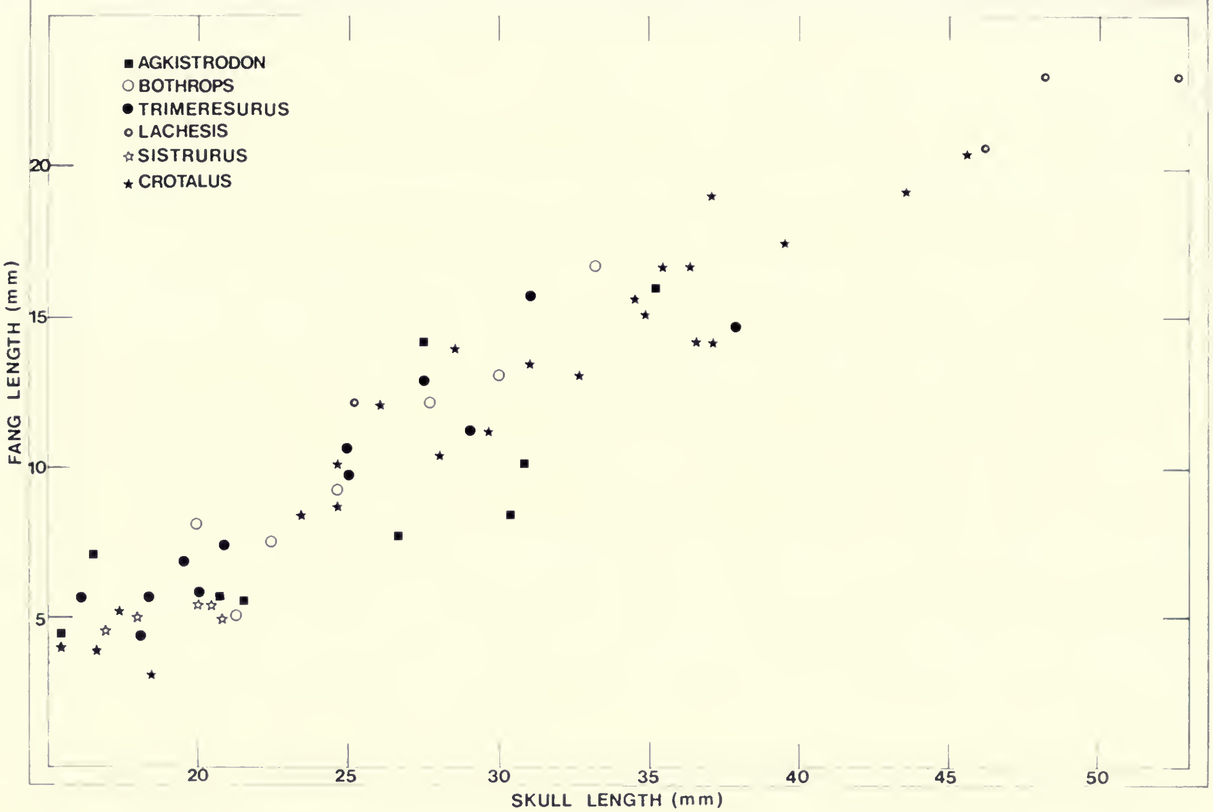

FIG. 44. Relation between longest maxillary tooth length and skull length in specimens of Crotalinae.

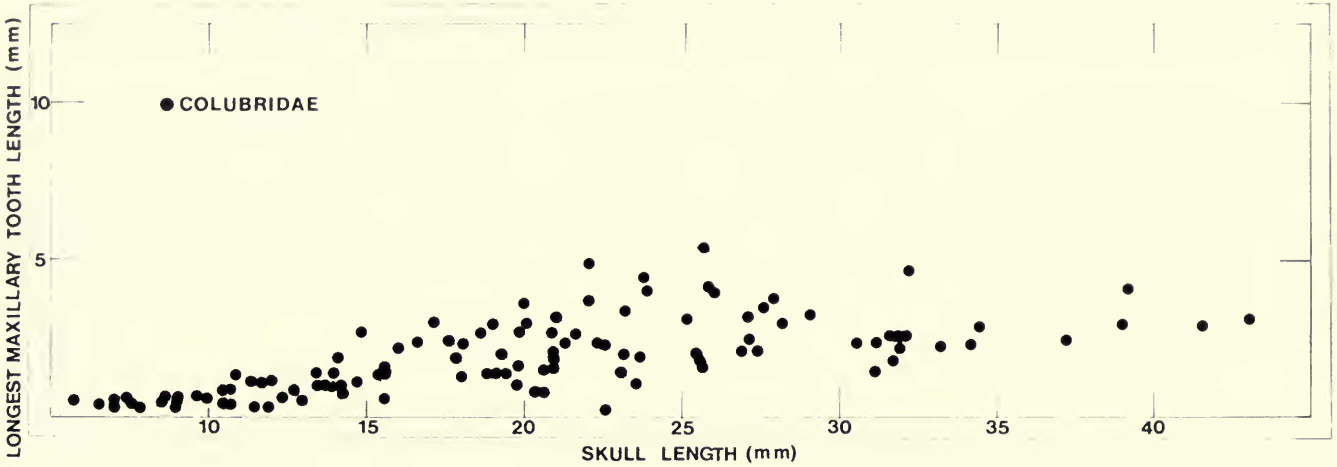

FIG. 45. Relation between longest maxillary tooth length and skull length in specimens of Colubridae.

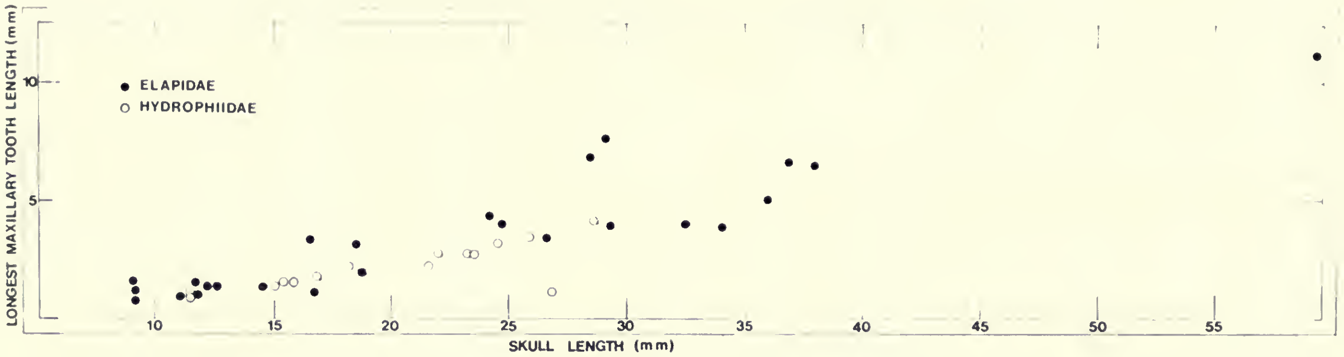

FIG. 46. Relation between longest maxillary tooth length and skull length in specimens of Elapidae and Hydrophiidae.

- Colubridae
  - *Boiga blandingi*
  - *Conopsis lineatus*
  - *Crotaphopeltis hotamboeia*
  - *Dispholidus typus*
  - *Enhydris chinensis*
  - *Erythrolamprus aesculapii*
  - *Heterodon platyrhinos*
  - *Holarchus albocinctus*
  - *Homalopsis buccata*
  - *Leptodeira annulata septentrionalis*
  - *Lioheterodon madagascariensis*
  - *Lystrophis d'orbignyi*
  - *Macropisthodon rudis*
  - *Opisthoplus degener*
  - *Philodryas schotti*
  - *Psammodynastes pulverulentus*
  - *Psammophis subtaeniatus*
  - *Rhamnophis aethiopissa*
  - *Theletornis kirtlandii*
  - *Tomodon dorsatus*
  - *Xenodon colubrinus*
- Elapidae
  - *Acanthophis antarcticus*
  - *Aspidelaps lubricus*
  - *Bungarus fasciatus*
  - *Dendroaspis angusticeps*
    - *viridis*
  - *Leptomicrurus collaris*
  - *Maticora bivirgata*
  - *Micrurus spixi*
  - *Naja naja*
  - *Notechis scutatus*
  - *Ophiophagus hannah*
  - *Walterinnesia aegyptia*
- Hydrophiidae
  - *Laticauda semifasciata*
- Viperinae
  - *Adenorhinos barbouri*
  - *Bitis peringueyi*
  - *Causus defilippii*
    - *lineatus*
    - *resimus*
    - *rhombeatus*
  - *Eristicophis macmahoni*
  - *Vipera aspis*
    - *berus*
    - *latasti*
    - *ursinii*
- Crotalinae
  - *Agkistrodon halys*
  - *Bothrops godmani*
  - *Crotalus lepidus*
  - *Sistrurus catenatus*
- *Azemiops*

In these colubrids this character state has a higher frequency of correlation with derived states of seven other characters compared to the frequency distribution of these states of the same seven characters in the total working sample (table 144) (Criterion 3).

TABLE 144. Correlation of State III of Character 45 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | |
|---|---|---|
| | In species having State III of Character 45 | In total working sample |
| 12 | 13.6% (3)* | 4.8% (13) |
| 22 | 13.6 (3) | 4.5 (11) |
| 33 | 76.2 (15) | 43.0 (76) |
| 41 | 31.3 (5) | 10.9 (20) |
| 42 | 28.6 (4) | 8.7 (14) |
| 44 | 19.0 (4) | 5.8 (11) |
| 46 | 68.2 (14) | 26.9 (52) |

* Number of genera.

TABLE 145. Habitat distribution of colubrid species having State III of Character 45 compared to the total colubrid working samlpe.

| | Total Working Sample | State III Character 45 |
|---|---|---|
| | % | % |
| Terrestrial | 36.2 | 40.9 |
| Arboreal | 16.5 | 40.9 |
| Aquatic | 14.9 | 9.1 |
| Subterrestrial | 10.8 | 4.5 |
| Fossorial | 12.4 | |
| Variation | 5.3 | 4.5 |
| Unknown | 3.5 | |

Also these colubrids have a markedly larger number of species confined to the arboreal habitat (40.9 per cent) compared to the relative abundance of arboreal colubrid species in the total working sample (16.5 per cent—table 145).

The application of two criteria (3, 5) suggests that State II is derived (Criterion 8).

The nature of this character (i.e., linearly ordered by size—table 142, column 2) makes the arrangement given of the four designated states the most probable.

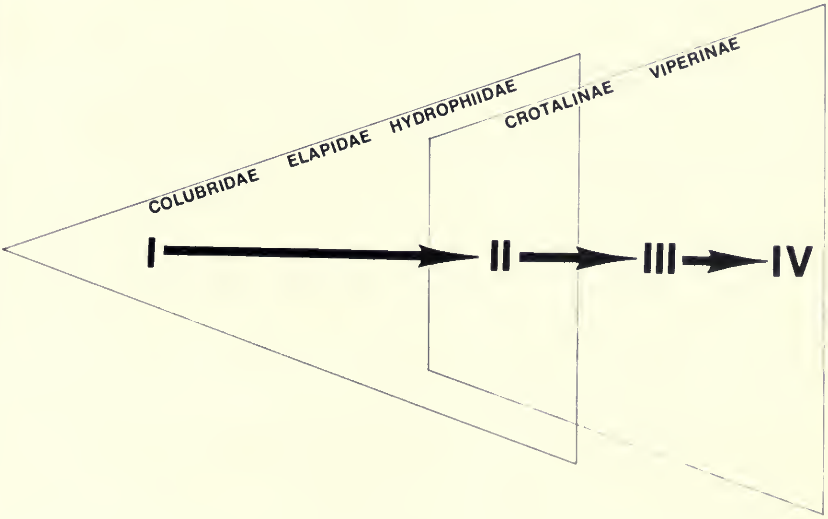

FIG. 47. Distribution among families of states of Character 45. Direction of change among states shown by arrows.

Our interpretation of the phyletics of Character 45 is shown in Figure 47.

## Character 46—Position of Fangs and Their Groove

### DESCRIPTION OF CHARACTER

See Peters (1964, p. 121) for a description of a fang. We recorded various positions of fangs on the maxilla plus the position of the venom groove on the fang. External groove and tubular canal are here considered the same part of the venom conducting apparatus, with location of the groove in the hollow fang taxa indicated by the "infolding" line. Gross size of teeth (fang) is not considered here; it appears to be differently distributed (Character 47). Relative size of the fang is discussed under Character 45. In this classification we were not concerned about number of teeth that were grooved; this information is noted, however, under States II and III.

Four states are recognized:

State I —fangs absent
State II —fangs anterior; groove anterior
State III—fangs posterior; groove anterior
State IV—fangs posterior; groove lateral

### FAMILIAL RANGES OF VARIATION (Table 146)

Colubridae—This family has States I, III, and IV in a sample of 309 species of 164 genera (571 skulls). State I occurs in 226 species of 112 genera (436 skulls), III in 64 species of 42 genera (95 skulls), IV in 19 species of 10 genera (40 skulls).

Elapidae—This family only has State II in a sample of 68 species of 38 genera (109 skulls).

Hydrophiidae—The sea snakes only have State II in a sample of 42 species of the 16 genera (143 skulls).

Viperinae, Crotalinae, *Azemiops*, *Atractaspis*—These four taxa all have State III in a sample of 84 species (33, 45, 1, 5 respectively) of the 16 genera (8, 6, 1, 1) (186 skulls: 94, 82, 2, 8).

### PHYLETICS OF CHARACTER 46

Fanged reptiles are almost exclusively restricted to the serpents and only in the advanced groups (Colubroidea: Colubridae, Elapidae, Hydrophiidae, Viperidae). We consider a fanged tooth (States II,

TABLE 146. Distribution of character states of the position of fangs.

| | STATES | | | |
|---|---|---|---|---|
| | II | I | III | IV |
| Description | Fangs anterior; grooved anterior | Fangs absent | Fangs posterior; grooved anterior | Fangs posterior; grooved lateral |
| | | SPECIES | | |
| Colubridae —309 | | 73.1% | 20.7% | 6.1% |
| Elapidae — 68 | 100.0% | | | |
| Hydrophiidae— 42 | 100.0 | | | |
| Viperinae — 33 | | | 100.0 | |
| Crotalinae — 45 | | | 100.0 | |
| *Azemiops* — 1 | | | 100.0 | |
| *Atractaspis* — 5 | | | 100.0 | |
| | | GENERA | | |
| Colubridae —164 | | 68.3 | 25.6 | 6.1 |
| Elapidae — 38 | 100.0 | | | |
| Hydrophiidae— 16 | 100.0 | | | |
| Viperinae — 8 | | | 100.0 | |
| Crotalinae — 6 | | | 100.0 | |
| *Azemiops* — 1 | | | 100.0 | |
| *Atractaspis* — 1 | | | 100.0 | |

III, IV) as derived because of its intimate function as part of the morphological specializations used in venom conduction (Criterion 4).

State II does not occur in the extant colubrids.

State II, anterior fangs with anterior groove, occurs in the following taxa:

Elapidae
*_Acanthophis antarcticus_
*_Apistocalamus lonnbergi_
*_loriae_
_Aspidelaps lubricus_
_scutatus_
*_Aspidomorphus lineaticollis_
*_muelleri_
**_Boulengerina annulata_
*_Brachyaspis curta_
**_Brachyurophis semifasciata_
**_Bungarus candidus_
**_fasciatus_
**_multicinctus_
**_Cacophis harriettae_
*_Calliophis japonicus_
**_Demansia olivacea_
**_textilis_
_Dendroaspis angusticeps_
_jamesoni_
_polylepis_
_viridis_
**_Denisonia coronoides_
**_fasciata_
**_nigrescens_
**_par_
**_superba_
**_woodfordi_
_Elapognathus minor_
_Elaps lacteus_
*_Elapsoidea sundevalli_
*_Furina diadema_
**_Glyphodon tristis_
_Hemachatus haemachatus_
**_Hoplocephalus bitorquatus_
**_bungaroides_

_Leptomicrurus collaris_
  _narducci_
_Maticora bivirgata_
**_Micropechis elapsoides_
  **_ikaheka_
*_Micruroides euryxanthus_
_Micrurus affinis_
  _fulvius_
  _lemniscatus_
  _mipartitus_
  _nigrocinctus_
  sp.
  _spixi_
*_Naja flava_
  *_haje_
  *_melanoleuca_
  *_naja_
  *_nigricollis_
  *_nivea_
*_Notechis scutatus_
**_Ogmodon vitianus_
*_Ophiophagus hannah_
*_Oxyuranus scutellatus_
*_Parapistocalamus hedigeri_
**_Pseudechis australis_
  **_porphyriacus_
*_Pseudohaje goldii_
  *_nigra_
*_Rhynchoelaps bertholdi_
*_Toxicocalamus stanleyanus_
**_Ultrocalamus preussi_
*_Vermicella annulata_
*_Walterinnesia aegyptia_
Hydrophiidae—all taxa

In this group there are forms that have solid teeth posterior to the fangs (*); forms with several maxillary teeth, all grooved or tubular (**); and forms having only a single fang.

We apply the uniqueness criterion (1) to Character State II for it is unique to derived stocks and therefore derived.

Bogert (1943) has argued for a progression in the elapids from a multiple toothed condition with all teeth grooved to a fang with ungrooved posterior companions, hence to a single fang. Hoffstetter (1962) and McDowell (1968, 1969) give other views.

Character State IV is rare and restricted to the colubrids (table 146) (Criterion 2). State IV, posterior fangs with lateral groove, occurs in the following colubrids:

Colubridae
_Chionactis occipitalis_
_Oxybelis aeneus_
  _argenteus_
  _brevirostris_
  _fulgidus_
_Passerita mycterizans_
  _nasuta_
  _prasinus_
_Psammodynastes pictus_
  _pulverulentus_
_Psammophis sibilans_
  _subtaeniatus_
_Pythonodipsas carinata_
_Sonora episcopa_
  _semiannulata_
_Stenorhina degenhardti_
_Tantilla gracilis_
_Tomodon dorsatus_
  _ocellatus_

In these colubrids this character state has a higher frequency of correlation with derived states of eight other characters compared to the frequency distribution of these states of the same eight characters in the total sample (table 147) (Criterion 3).

TABLE 147. Correlation of States III and IV of Character 46 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State III of Character 46 | In species having State IV of Character 46 | In total working sample |
| 2 | | 47.4% (4) | 15.6% (31) |
| 4 | 15.6% (2) | | 3.8 (4) |
| 7 | | 42.1 (5) | 25.5 (56) |
| 13 | 45.3 (17) | | 31.8 (54) |
| 25 | | 20.0 (2) | 6.3 (12) |
| 26 | 43.2 (5) | 40.0 (4) | 12.6 (19) |
| 27 | | 33.3 (4) | 17.9 (40) |
| 31 | 46.0 (20) | | 19.5 (44) |
| 32 | | 47.1 (5) | 26.3 (55) |
| 33 | | 76.5 (8) | 43.0 (76) |
| 40 | | 42.1 (7) | 24.8 (54) |

* Number of genera.

Also these colubrids have a markedly larger number of species of arboreal and fossorial habits (68.5 per cent) compared to the relative abundance of arboreal and fossorial colubrid species in the total sample (28.9 per cent—table 148) (Criterion 5).

TABLE 148. Habitat distribution of colubrid species having States III and IV of of Character 46 compared to the total colubrid working sample.

| | Total working sample | Character 46 | |
|---|---|---|---|
| | | State III | State IV |
| Terrestrial | 36.2% | 28.1% | 15.8% |
| Arboreal | 16.5 | 40.6 | 47.4 |
| Aquatic | 14.9 | 6.3 | |
| Subterrestrial | 10.8 | 6.3 | 5.3 |
| Fossorial | 12.4 | 10.9 | 21.1 |
| Variation | 5.3 | | 10.5 |
| Unknown | 3.5 | 7.8 | |

The application of four criteria (2–5) suggests that this state is derived. The fossorial species are all North American taxa representing three genera (*Chionactis, Sonora, Stenorhina*) and this character state may reflect a monophyletic origin for this group.

State III is not particularly rare in the colubrids (20.7 per cent—table 146).

State III, posterior fangs with anterior groove, occurs in the following colubrids (plus other taxa):

- Colubridae
  - *Aparallactus lunulatus*
    - *werneri*
  - *Apostolepis ambinigra*
  - *Boiga blandingi*
    - *cynodon*
    - *dendrophila*
    - *irregularis*
    - *jaspidea*
    - *kraepelini*
    - *multimaculata*
    - *pulverulentus*
    - *trigonatus*
  - *Calamelaps unicolor*
  - *Chilomeniscus cinctus*
  - *Chilorhinophis carpenteri*
  - *Chrysopelea ornata*
  - *Clelia clelia*
    - *fitzingeri*
    - *petola*
  - *Coniophanes fissidens*
  - *Conophis lineatus*
  - *Crotaphopeltis hotamboeia*
  - *Dipsadoboa unicolor*
  - *Dispholidus typus*
  - *Drepanoides eatonii*
  - *Dromophis lineatus*
    - *praeornata*
  - *Elapomorphus blumii*
  - *Enhydris chinensis*
    - *enhydris*
    - *plumbea*
  - *Erythrolamprus aesculapii*
  - *Homalopsis buccata*
  - *Ialtris dorsalis*
  - *Imantodes cenchoa*
  - *Leptodeira annulata*
    - *maculata*
    - *septentrionalis*
  - *Malpolon moilensis*
    - *monspessulanus*
  - *Manolepis putmani*
  - *Mimophis mahfalensis*
  - *Miodon gabonensis*
  - *Opisthoplus degener*
  - *Oxyrhopus petola*
  - *Philodryas schotti*
  - *Psammophylax rhombeatus*
  - *Pseudoboa claelia*
    - *clathrata*
    - *haasi*
    - *neuwiedii*
  - *Pseudotomodon trigonatus*
  - *Rhacidelus brazili*
  - *Rhamphiophis oxyrhynchus*
  - *Rhinobothryum bovalli*
  - *Rhinostoma guianense*
  - *Siphlophis cervinus*
  - *Tachymenis chilensis*
    - *peruviana*
  - *Telescopus iberus*
    - *semiannulatus*
  - *Thelotornis kirtlandii*
  - *Trimorphodon lambda*
  - *Tripanurgos compressus*
- Viperinae—all taxa
- Crotalinae—all taxa
- *Azemiops*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of four other characters compared to the frequency distribution of these states of the same four characters in the total sample (table 147) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the arboreal habitat (40.6 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent—table 148) (Criterion 5).

The application of three criteria (3–5) suggests that this state is derived (Criterion 8).

Only five species of all the rear-fanged snakes have very few solid teeth posterior to their fangs. They are:

*Boiga blandingi*
*cyanodon*

*Chilomeniscus cinctus*
*Crotaphopeltis hotamboeia*
*Dipsadoboa unicolor*

These species represent the Orient, Africa, and the New World, and are terrestrial, arboreal, and fossorial. There is no particular correlation to this characteristic, with so few snakes distributed over a wide geographic range and in such diverse habitat zones.

However, with practically every rear-fanged snake having the grooved (and almost invariably enlarged) teeth at the posterior end of the maxilla, it appears that the elapids, with their anterior fangs, probably did not arise from a rear-fanged snake, and vice versa. McDowell (1968, 1969) and Hoffstetter (1962) give a contrary view.

The two kinds of rear-fanged snakes (III, IV) probably evolved independently from the primitive State I because the colubrid spe-

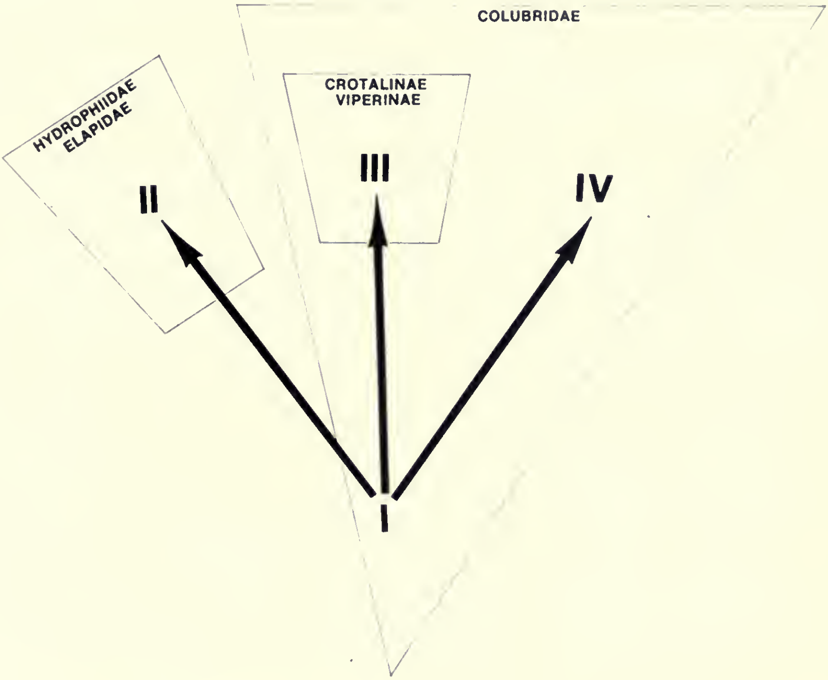

FIG. 48. Distribution among families of states of Character 46. Direction of change among states shown by arrows.

cies with each of these states correlate mostly with derived states of different characters (table 147).

The positional relationship of the fangs is clear in multiple-toothed elapids, hydrophiids and colubrids. It is inferential and rather conjectural in taxa having but a single fang and no other teeth. For the elapids the case can be argued through annectant forms in the family. For the viperids other evidence must be brought to bear to show a likely posterior fang origin. We here accept the arguments of Boulenger (1915), Anthony (1955), and Haas (1931), that Kockva (1965) has reinforced, contrary to the opinions cited in Marx and Rabb (1965). A parallel to the viperid situation exists among the aparallactine colubrids, with the important difference that annectant multiple-toothed taxa still exist. The phylogenetic and morphological problems in this group have recently been given attention (Bourgeois, 1965; McDowell, 1968; Kochva and Wollberg, 1970), but much has yet to be learned.

Our interpretation of the phyletics of Character 46 is shown in Figure 48.

## Character 47—Position of Enlarged Maxillary Teeth

### DESCRIPTION OF CHARACTER

Enlarged teeth on the maxilla and the position of these larger teeth were recorded. The enlarged maxillary teeth may or may not show modifications for conducting venom, which are therefore considered separately (Character 46). In the cases of the venomous taxa possessing but a single tooth on the maxilla, the judgment concerning enlargement was based on the sizes of the dentary teeth.

Six states are recognized:

State I —no enlarged teeth
State II —enlarged anterior teeth
State III—enlarged posterior teeth
State IV—enlarged anterior and posterior teeth
State V —enlarged medial and posterior teeth
State VI—enlarged medial teeth

### FAMILIAL RANGES OF VARIATION (Table 149)

Colubridae—This family has all six states in a sample of 309 species of 164 genera (568 skulls). State I occurs in 120 species of 63

TABLE 149. Distribution of character states of the enlargement of maxillary teeth.

| | STATES | | | | | | |
|---|---|---|---|---|---|---|---|
| | I | II | III | IV | V | VI | |
| Description | None | Anterior | Posterior | Anterior & Posterior | Medial & Posterior | Medial | |
| | | | SPECIES | | | | |
| Colubridae —309 | 38.8% | 0.3% | 51.5% | 2.3% | 5.5% | 1.6% | |
| Elapidae — 69 | 1.4 | 98.6 | | | | | |
| Hydrophiidae— 42 | | 100.0 | | | | | |
| Viperinae — 33 | | | 100.0 | | | | |
| Crotalinae — 45 | | | 100.0 | | | | |
| *Azemiops* — 1 | | | 100.0 | | | | |
| *Atractaspis* — 5 | | | 100.0 | | | | |
| | | | GENERA | | | | INTRAGENERIC VARIATION |
| Colubridae —164 | 33.5 | 0.6 | 49.4 | 2.4 | 6.1 | 2.4 | 5.5%* |
| Elapidae — 38 | 2.6 | 97.4 | | | | | |
| Hydrophiidae— 16 | | 100.0 | | | | | |
| Viperinae — 8 | | | 100.0 | | | | |
| Crotalinae — 6 | | | 100.0 | | | | |
| *Azemiops* — 1 | | | 100.0 | | | | |
| *Atractaspis* — 1 | | | 100.0 | | | | |

* I, III=7 genera; I, IV=1; III, IV=1.

genera (237 skulls), II in *Boaedon lineatus* (5 skulls), III in 159 species of 89 genera (273 skulls), IV in 7 species of 6 genera (16 skulls), V in 17 species of 10 genera (29 skulls), and State VI in 5 species of 4 genera (8 skulls).

Intrageneric variation occurs in 9 genera: *Coluber, Drymobius, Lampropeltis, Masticophis, Natrix, Oxybelis, Salvadora* (I, III); *Alsophis* (III, IV); *Storeria* (I, IV).

Elapidae—This family has States I and II in a sample of 69 species of 38 genera (111 skulls). State I occurs in monotypic *Ogmodon* (1 skull), II in 68 species of 37 genera (110 skulls).

Hydrophiidae—The sea snakes only have State II in a sample of 42 species of the 16 genera (143 skulls).

Viperinae, Crotalinae, *Azemiops, Atractaspis*—The true vipers, pit vipers, *Azemiops*, and *Atractaspis* all have State III in a sample of 84 species (33, 45, 1, 5 respectively) of the 16 genera (8, 6, 1, 1) (186 skulls: 94, 82, 2, 8).

### Phyletics of Character 47

Character States II, IV, V, and VI are rare in the colubrids (table 149) (Criterion 2).

Except for a single colubrid, *Boadeon lineatus*, State II is restricted to the elapids (except *Ogmodon*) and hydrophiids (Criterion 7), which indicates that this state is derived.

State IV, enlarged anterior and posterior maxillary teeth, occurs in the following colubrid taxa:

Colubridae
- *Alsophis sanctae-crucis*
- *Lycodon aulicus*
  - *striatus*
- *Pythonodipsas carinata*
- *Spalerosophis diadema*
- *Storeria dekayi*
- *Trimorphodon lambda*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total sample (table 150) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the terrestrial habitat (71.4 per cent) compared to the relative abundance of terrestrial colubrid species in the total sample (36.2 per cent—table 151) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that this state is derived (Criterion 8).

TABLE 150. Correlation of States I, III, IV, and V of Character 47 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | | |
|---|---|---|---|---|---|
| | In species having State III | In species having State I | In species having State V | In species having State IV | In total working sample |
| 1 | | 20.0% (16)* | | | 14.3% (28) |
| 7 | | 40.0 (31) | | 42.9% (3) | 25.5 (56) |
| 11 | | | 47.1% (6) | 42.9 (3) | 26.7 (50) |
| 13 | | | 64.7 (6) | | 31.8 (54) |
| 16 | | 34.2 (15) | | | 21.7 (34) |
| 17 | | 54.2 (26) | | | 35.4 (48) |
| 20 | | | | 71.4 (5) | 41.2 (74) |
| 21 | | | | 50.0 (3) | 18.9 (29) |
| 26 | | | 30.0 (2) | | 12.6 (19) |
| 27 | | | 50.0 (6) | | 17.9 (40) |
| 31 | | | 35.3 (5) | 42.9 (3) | 19.5 (44) |
| 32 | 36.0% (31) | | 38.5 (2) | | 26.3 (55) |
| 33 | | | 75.0 (6) | | 43.0 (76) |
| 40 | | | | 42.9 (2) | 24.8 (54) |
| 46 | 41.1 (41) | | 76.5 (7) | | 26.9 (52) |
| 50 | | 30.0 (14) | | | 20.0 (24) |

* Number of genera.

TABLE 151. Habitat distribution of colubrid species having certain states of Character 47 compared to the total colubrid sample.

| | | CHARACTER 47 STATES | | | |
|---|---|---|---|---|---|
| | Total working sample | III | I | IV | V |
| Terrestrial | 36.2% | 38.1% | 26.7% | 71.4% | 41.2% |
| Arboreal | 16.5 | 20.0 | 10.8 | | 41.2 |
| Aquatic | 14.9 | 12.5 | 21.7 | | |
| Subterrestrial | 10.8 | 7.5 | 15.0 | 28.6 | 5.9 |
| Fossorial | 12.4 | 10.6 | 17.5 | | |
| Variation | 5.3 | 4.4 | 7.5 | | 11.8 |
| Unknown | 3.5 | 6.3 | 0.8 | | |

State VI, enlarged medial maxillary teeth, occurs in the following colubrid taxa:

*Dryocalamus davisoni*
*Lamprophis aurora*
*Lycophidion capense*
*Mehelya capensis*
  *poensis*

Four of these five colubrids are from tropical Africa (Criterion 6).

The application of two criteria (2, 6) suggests that this state is derived (Criterion 8).

State V, enlarged medial and posterior maxillary teeth, occurs in the following colubrids:

Colubridae
*Cyclocorus lineatus*
*Dinodon rufozonatus*
*Dromophis lineatus*
  *praeornata*
*Mimophis mahfalensis*
*Passerita mycterizans*
  *nasuta*
  *prasinus*
*Psammodynastes pictus*
  *pulverulentus*
*Psammophis sibilans*
  *subtaeniatus*
*Siphlophis cervinus*
*Stegonotus borneensis*
  *magnus*
*Telescopus iberus*
  *semiannulatus*

In these colubrids this character state has a higher frequency of correlation with derived states of eight other characters compared to the frequency distribution of these states of the same eight characters in the total sample (table 150) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the arboreal habitat (41.2 per cent) compared to the relative abundance of arboreal colubrid species in the total sample (16.5 per cent—table 151) (Criterion 5).

TABLE 152. Geographic distribution of colubrid species having certain states of Character 47 compared to the total colubrid sample.

| | Total working sample | Character 47 STATES | | | |
|---|---|---|---|---|---|
| | | III | I | IV | V |
| United States | 17.2% | 11.3% | 28.3% | 14.3% | |
| South America | 17.8 | 24.4 | 13.3 | | 5.9% |
| Central America | 6.7 | 9.4 | 5.0 | | |
| Mexico | 7.0 | 6.3 | 10.0 | 14.3 | |
| Caribbean | 3.5 | 5.0 | 1.7 | 14.3 | |
| New World, intra-regional | 1.9 | 3.1 | 0.8 | | |
| Tropical Africa | 14.3 | 14.5 | 9.2 | 14.3 | 23.5 |
| Northern Africa & Sahara | 1.3 | 2.5 | | | |
| Europe | 1.6 | 1.3 | 0.8 | | |
| Southwestern Asia & Pakistan | 2.5 | 3.1 | 1.7 | | 5.9 |
| India, Ceylon, Nepal | 2.9 | 2.5 | 2.5 | 14.3 | |
| Eastern Asia | 10.8 | 8.8 | 15.0 | | 5.9 |
| Southeastern Asia | 1.9 | 1.3 | 1.7 | | 5.9 |
| Indo-Australia, Phil. Ids. | 4.8 | 3.1 | 4.2 | 14.3 | 23.5 |
| Moluccan | 0.6 | 0.6 | 0.8 | | |
| New Guinea-New Britain | 0.6 | 0.6 | | | 5.9 |
| Madagascar | 1.3 | 1.3 | 0.8 | | 5.9 |
| Old World, intra-regional | 3.2 | 0.6 | 4.2 | 14.3 | 17.6 |

These colubrids have a markedly larger number of species confined to tropical Africa and the Indo-Australian regions (47.0 per cent), all but one species are from the Old World, compared to the relative abundance of colubrid species from the overall sample (19.1 per cent—table 152) (Criterion 6).

The application of four criteria (2, 3, 5, 6) strongly suggests that this state is derived (Criterion 8).

Character States I and III are both common in the colubrids (38.8 per cent and 51.5 per cent—table 149).

The colubrids with State I have a larger number of species confined to the aquatic habitat (21.7 per cent) compared to the relative abundance of aquatic colubrid species in the total sample (14.9 per cent—Criterion 5), whereas this is not true for State III (table 151).

In addition, the colubrids with State I have a significantly larger number of species confined to the United States (28.3 per cent) compared to the relative abundance of United States colubrids in the total sample (17.2 per cent—Criterion 6), whereas this is not true for State III (table 152).

In the colubrids Character State I has a higher frequency of correlation with derived states of five other characters compared to the frequency distribution of these states of the same five characters in the total sample (Criterion 3), whereas this is true for two characters with State III (table 150).

The application of three criteria (3, 5, 6) in State I suggests that this state is derived compared to State III because only a single criterion is applicable to State III. In addition, State III only has positive correlation with two other characters compared to the positive correlation of State I with five characters.

State I, no enlarged maxillary teeth, occurs in the following taxa:

- Colubridae
  - *Abastor erythrogrammus*
  - *Achalinus spinalis*
  - *Arizona elegans*
  - *Aspidura trachyprocta*
  - *Atractus elaps*
    - *erythromelas*
    - *latifrons*
    - *ventrimaculatus*
  - *Bothrophthalmus lineatus*
  - *Brachyorrhus albus*
  - *Calamaria leucogaster*
    - *linnaei*
    - *pavimentata*
    - *schlegeli*
    - *septentrionalis*
  - *Carphophis amoena*
  - *Chilomeniscus cinctus*
    - *fasciatus*
  - *Chironius carinatus*
    - *fuscus*
  - *Chrysopelea ornata*
  - *Coluber constrictor*
    - *jugularis*
    - *najadum*
  - *Conopsis lineatus*
    - *nasus*
  - *Dasypeltis fasciatus*
    - *inornatus*
    - *scabra*
  - *Dimades plicatilis*
  - *Dromicodryas bernieri*
  - *Dryadophis amarali*
    - *boddaerti*
  - *Drymarchon corais*
  - *Drymobius bifossatus*
  - *Duberria lutrix*
  - *Elaphe carinata*
    - *dione*
    - *flavirufa*
    - *frenatus*
    - *guttata*
    - *mandarina*
    - *obsoleta*
    - *porphyracea*
    - *radiata*
    - *rufodorsata*
    - *schrencki*
    - *subocularis*
    - *taeniura*
    - *vulpina*
  - *Farancia abacura*
  - *Ficimia publia*
  - *Geophis multitorques*
    - *semidoliatus*
  - *Gonyosoma oxycephalum*
  - *Grayia smithi*
  - *Haldea striatula*
    - *valeriae*
  - *Holuropholis olivaceus*
  - *Hydraethiops melanogaster*
  - *Hydrops triangularis*
  - *Hypsirhynchus ferox*
  - *Lampropeltis getulus*
  - *Liopeltis tricolor*
  - *Lycodonomorphus bicolor*
  - *Macrocalamus lateralis*
  - *Masticophis flagellum*
  - *Natrix aequifasciata*
    - *annularis*
    - *anoscopus*
    - *cyclopion*
    - *erythrogaster*
    - *kirtlandi*
    - *percarinata*
    - *rhombifera*
    - *septemvittata*
    - *sipedon*
    - *taxispilota*

*Ninia atrata*
  *sebae*
*Opheodrys aestivus*
  *major*
  *vernalis*
*Opisthotropis kuatunensis*
  *latouchi*
*Oxybelis brevirostris*
*Oxyrhabdium modestum*
*Pituophis deppei*
  *melanoleucus*
  *sayi*
*Pseudorhabdion collaris*
*Pseustes poecilonotus*
  *sulphureus*
*Ptyas korros*
  *mucosus*
*Rhynchocalamus melanocephalus*
*Salvadora lemniscata*
*Scaphiodontophis annulatus*
*Scaphiophis albopunctatus*
*Sibon sibon*
*Sibynomorphus turgidus*
*Simophis rhinostoma*
*Spilotes pullulatus*
*Stilostoma extenuatum*
*Storeria occipitomaculata*
*Thamnophis butleri*
  *eques*
  *marcianus*
  *macrostemma*
  *radix*
  *sauritus*
  *sirtalis*
*Tretanorhinus mocquardi*
  *variabilis*
*Trirhinopholis styani*
*Tropidocloniom lineatum*
*Tropidodipsas fischeri*
  *philippi*
*Zaocys dhumnades*
  *nigromarginatus*
Elapidae
  *Ogmodon vitianus*

States I, IV, and V probably did not evolve from each other. The colubrids with each of these states are predominantly abundant in different habitat zones (table 151), correlate mostly with derived states of different characters (table 150), and where significant (I, V) are more abundant in different geographic areas (table 152).

The other two derived states (II, VI) are extremely rare and give little direct clue to their sequential direction. However, if all derived states do stem from State III, then II and VI form end points of morphological sequences through IV and V, respectively.

State II, enlarged anterior teeth, occurs in the following taxa in our working sample:

Colubridae
  *Boaedon lineatus*
Elapidae
  all taxa except *Ogmodon.*
Hydrophiidae—all taxa

State VI, enlarged medial teeth, occurs in the following colubrids in our working sample:

Colubridae
  *Dryocalamus davisoni*
  *Lamprophis aurora*
  *Lycophidion capense*
  *Mehelya capensis*
    *poensis*

Our interpretation of the phyletics of Character 47 is shown in Figure 49.

## Character 48—Number of Palatine Teeth

### Description of Character

The palatines are a pair of dentigerous bones located in the anterior roof of the mouth, medial to the maxillaries and usually articulating posteriorly with the pterygoids. The number of teeth (or tooth sockets) on the palatine bones was counted. Each bone was scored separately.

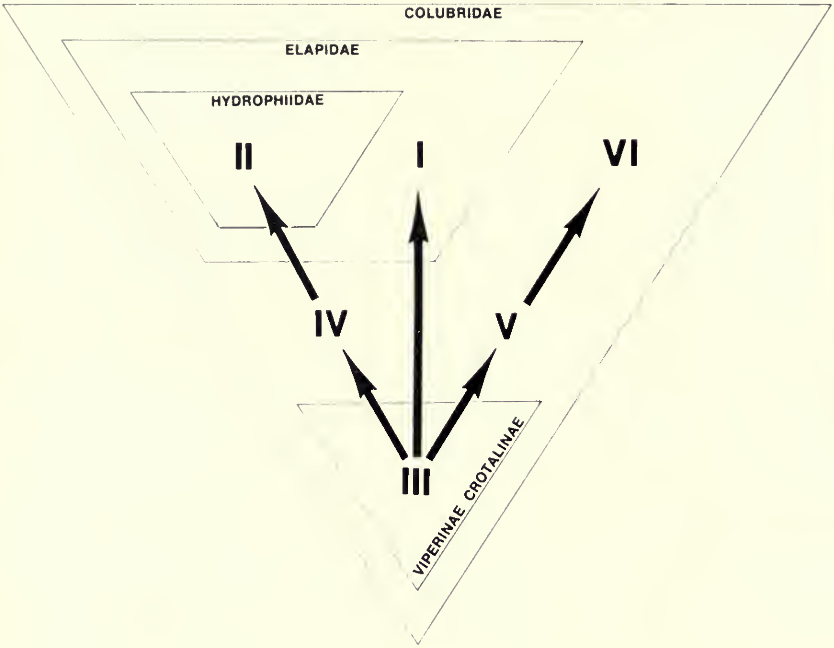

Fig. 49. Distribution among families of states of Character 47. Direction of change among states shown by arrows.

### Classes and States

The total range of variation in number of palatine teeth is segmented in steps of three, since a span of three covers most of the intraspecific variation encountered (88.5 per cent—table 153). Eight classes resulted as shown in Table 154. The mean of each taxon was assigned to a class (table 154). States were established when there was a marked change in frequency of number of species between classes, with special reference to the distribution among the viperids.

TABLE 153. Spans in number of palatine teeth by species and families.

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae[1] | Hydrophiidae | Viperinae[2] | Crotalinae |
| 1 | 170 | 81 | 16 | 21 | 19 | 33 |
| 2 | 129 | 76 | 21 | 10 | 12 | 10 |
| 3 | 55 | 34 | 10 | 8 | 2 | 1 |
| 4 | 23 | 16 | 6 | 1 |  |  |
| 5 | 12 | 10 | 2 |  |  |  |
| 6 | 4 | 4 |  |  |  |  |
| 7 | 3 | 3 |  |  |  |  |
| 8 | 3 | 3 |  |  |  |  |
| 11 | 1 | 1 |  |  |  |  |
| Totals | 400 | 228 | 55 | 40 | 33 | 44 |
| Span 3 or less | 88.5% | 83.8% | 85.5% | 97.5% | 100.0% | 100.0% |

[1] Including part of Bogert, 1943, table 2.

[2] Excluding *Azemiops* and *Atractaspis*.

TABLE 154. Frequency distribution of species in range classes of number of palatine teeth in families of advanced snakes.

| | | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| Classes | Range | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 0 – 2.49 | 1/0 | | 2/1 | 9/2 | 9/0 |
| 2 | 2.50– 5.49 | 16/7 | 7/7 | 5/1 | 19/5 | 35/6 |
| 3 | 5.50– 8.49 | 45/28 | 19/11 | 27/11 | 4/1 | |
| 4 | 8.50–11.49 | 91/50 | 16/9 | 6/3 | 1/0 | |
| 5 | 11.50–14.49 | 37/12 | 9/9 | | | |
| 6 | 14.50–17.49 | 18/8 | 4/2 | | | |
| 7 | 17.50–20.49 | 17/10 | | | | |
| 8 | 20.50–23.49 | 3/2 | | | | |
| Totals | | 228/117 | 55/38 | 40/16 | 33/8 | 44/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

Three states are recognized:

State I —Classes 3–8 (5.5–23.49)
State II —Class 2 (2.5–5.49)
State III—Class 1 (0–2.49)

A fourth state could be recognized for class 8, the high extreme in the colubrids, but only 1.5 per cent of the species would fall in this category. In the other tooth number characters, the extreme states are represented by 4–6 per cent of the taxa.

### Familial Ranges of Variation (Table 155)

Colubridae—This family has all three states in a sample of 816 palatine bones from 431 skulls of 228 species of 117 genera. State I occurs in 211 species and 110 genera, II in 16 species and 7 genera, III in one species.

TABLE 155. Distribution of character states of the number of palatine teeth.

| | STATES | | |
|---|---|---|---|
| | I | II | III |
| Classes[1] | 3–8 | 2 | 1 |
| | | SPECIES | |
| Colubridae —228 | 92.5% | 7.0% | 0.4% |
| Elapidae — 55 | 87.3 | 12.7 | |
| Hydrophiidae— 40 | 82.5 | 12.5 | 5.0 |
| Viperinae — 33 | 15.2 | 57.6 | 27.3 |
| Crotalinae — 44 | | 79.5 | 20.5 |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 5 | | 40.0 | 60.0 |
| | | GENERA | |
| Colubridae —117 | 94.0 | 6.0 | |
| Elapidae — 38 | 81.6 | 18.4 | |
| Hydrophiidae— 16 | 87.5 | 6.3 | 6.3 |
| Viperinae — 8 | 12.5 | 62.5 | 25.0 |
| Crotalinae — 6 | | 100.0 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 1 | | | 100.0 |

[1] See Table 154.

The range in the number of palatine teeth is from 2 (*Lytorhynchus paradoxus*) to 22 (*Mehelya poensis*).[1] The maximum span in a single species is 11 (*Storeria dekayi*). However, 83.8 per cent of the species have a span of 3 or less (table 153). The maximum span in a single specimen is 5 (*Storeria occipitomaculata*—FMNH 98592).

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[1] Dr. Donald G. Broadley kindly informed us (*personal communication*) that he has specimens of four species of *Amblyodipsas* and *Xenocalamus* that lack palatine teeth.

Elapidae—This family has States I and II in a sample of 195 palatine bones from 101 skulls of 55 species of 38 genera. State I occurs in 48 species and 31 genera, II in 7 species and 7 genera.

The range in the number of palatine teeth is from 3 (*Brachyurophis semifasciata*) to 17 (*Demansia psammophis, Pseudechis porphyriacus*). However, 88.5 per cent of the species have a span of 3 or less (table 153). The maximum span in a single specimen is 4 (4 species of 3 genera).

Hydrophiidae—The sea snakes have all three states in a sample of 240 palatine bones from 125 skulls of 40 species of the 16 genera. State I occurs in 33 species and 14 genera, II in 5 species and 1 genus, III in 2 species and 1 genus.

The range in the number of palatine teeth is from 0 (*Emydocephalus annulatus, E. ijimae*) to 12 (*Aipysurus eydouxi*). The maximum span in a single species is 4 (*Pelamis platurus*). However, 97.5 per cent of the species have a span of 3 or less (table 153). The maximum span in a single specimen is 3 (4 species of 4 genera).

Viperinae—The true vipers have all three states in a sample of 171 palatine bones from 92 skulls of 33 species of the 8 genera. State I occurs in 5 species and 1 genus, II occurs in 19 species and 5 genera, III occurs in 9 species and 2 genera.

The range is from 0 (*Echis coloratus*) to 9 (*Causus lichtensteini, C. rhombeatus*). The maximum span is 3 (*Bitis arietans, Echis coloratus*). All the species have a span of 3 or less (table 153). The maximum span in a single specimen is 2 (6 species of 3 genera).

Crotalinae—The pit vipers have States II and III in a sample of 143 palatine bones from 76 skulls of 44 species of the 6 genera. State II occurs in 35 species and 6 genera, State III in 9 species.

The range is from 0 (*Agkistrodon rhodostoma, Trimeresurus flavoviridis, T. mucrosquamatus*) to 5 (7 species of 3 genera). The maximum span is 3 (*Bothrops atrox*). All the species have a span of 3 or less (table 153). The maximum span in a single specimen is 2 (6 species of 4 genera).

*Azemiops* has State II as sampled from 4 palatine bones of 2 skulls; each bone has 4 teeth.

*Atractaspis* has States II and III in a sample of 12 palatine bones from 6 skulls of 5 species. State II occurs in 2 species, III in 3 species.

The range in number of palatine teeth is from 1 (*A. corpulenta, A. irregularis*) to 4 (*A. microlepidota*). The maximum span in a single species is 2 (3 species). The maximum span in a single specimen is 2 (3 species).

### PHYLETICS OF CHARACTER 48

Character States II and III are rare in the colubrids (table 155) (Criterion 2).

State II, a low number of palatine teeth, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Atractus elaps*
  - *Calamaria linnaei*
  - *Heterodon nasicus*
    - *simus*
  - *Holarchus cyclurus*
  - *Lystrophis d'orbignyi*
    - *semicinctus*
  - *Lytorhynchus diadema*
    - *gaddi**
    - *maynardi*
    - *ridgewayi**
  - *Malpolon moilensis*
  - *Phyllorhynchus decurtatus*
  - *Pythonodipsas carinata*
  - *Rhamphiophis oxyrhynchus*
  - *Tomodon dorsatus*
- Elapidae
  - *Brachyaspis curta*
  - *Brachyurophis semifasciata*
  - *Dendroaspis angusticeps*
  - *Hemachatus haemachatus*
  - *Ogmodon vitianus*
  - *Parapistocalamus hedigeri*
  - *Vermicella annulata*
- Hydrophiidae
  - *Aipysurus foliosquama*
    - *laevis*
  - *Laticauda* (4)
- Viperinae
  - *Adenorhinos barbouri*
  - *Atheris* (5)
  - *Cerastes*(2)
  - *Echis carinatus*
  - *Eristicophis macmahoni*
  - *Vipera*(9)
- Crotalinae
  - *Agkistrodon acutus*
    - *bilineatus*
    - *contortrix*
    - *halys*
    - *hypnale*
    - *nepa*
    - *piscivorus*
    - *strauchi*
  - *Bothrops atrox*
    - *barnetti*
    - *dunni*
    - *godmani*
    - *jararacussu*
    - *neuwiedi*
    - *schlegeli*
  - *Crotalus adamanteus*
    - *atrox*
    - *cerastes*
    - *horridus*
    - *lepidus*
    - *mitchelli*
    - *pusillus*
    - *ruber*
    - *viridis*
  - *Lachesis mutus*
  - *Sistrurus*(2)
  - *Trimeresurus albolabris*
    - *monticola*
    - *okinavensis*
    - *puniceus*
    - *stejnegeri*
    - *sumatranus*
    - *wagleri*
- *Azemiops*
- *Atractaspis bibroni*
  - *microlepidota*

*Not in working sample.

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to

TABLE 156. Correlation of State II of Character 48 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | | |
|---|---|---|---|---|
| | In species having State II of Character 48 | | In total working sample | |
| 1 | 42.9% | (4)* | 14.3% | (28) |
| 2 | 71.4 | (7) | 15.6 | (31) |
| 9 | 28.6 | (3) | 6.8 | (14) |
| 12 | 35.7 | (4) | 4.8 | (13) |
| 22 | 21.4 | (3) | 4.5 | (11) |
| 32 | 58.3 | (6) | 26.3 | (55) |

* Number of genera.

the frequency distribution of these states of the same six characters in the total sample (table 156) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the terrestrial and fossorial habitats (57.1 per cent, 35.7 per cent) compared to the relative abundance of terrestrial and fossorial colubrid species in the total sample (36.2 per cent, 12.4 per cent—table 157) (Criterion 5).

TABLE 157. Habitat distribution of colubrid species having State II of Character 48 compared to the total working sample.

| | Total Working Sample % | State II Character 48 % |
|---|---|---|
| Terrestrial | 36.2 | 57.1 |
| Arboreal | 16.5 | 7.1 |
| Aquatic | 14.9 | |
| Subterrestrial | 10.8 | |
| Fossorial | 12.4 | 35.7 |
| Variation | 5.3 | |
| Unknown | 3.5 | |

The application of three criteria (2, 3, 5) suggests that State II is derived (Criterion 8).

State III, minimum number of palatine teeth, occurs in the colubrid *Lytorhynchus paradoxus* (not in working sample) and the following species in our working sample:

Hydrophiidae
  *Emydocephalus*(2)

Viperinae
  *Bitis*(8)
  *Echis coloratus*
Crotalinae
  *Agkistrodon rhodostoma*

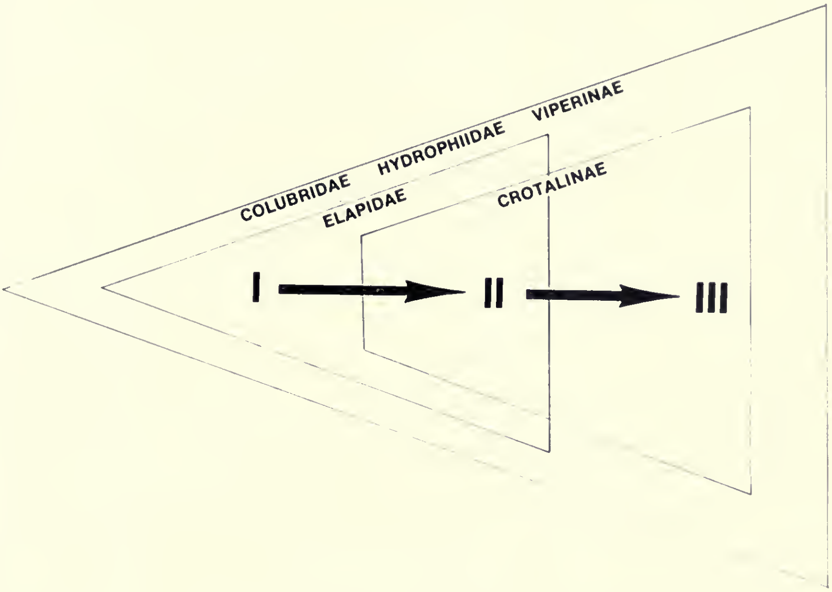

FIG. 50. Distribution among families of states of Character 48. Direction of change among states shown by arrows.

*Bothrops alternatus*
*cotiara*
*lansbergii*
*Crotalus durissus*
*molossus*
*Trimeresurus flavoviridis*
*jerdoni*
*mucrosquamatus*
*Atractaspis corpulenta*
*dahomeyensis*
*irregularis*

This extremely rare state is considered derived (Criterion 2).

The serial nature of this character (i.e., numerical order—table 154, column 2) makes the phyletic arrangement given of the three designated states the most probable (fig. 50). For further remarks on the variation in this character see Marx and Rabb (1970).

## Character 49—Number of Pterygoid Teeth

### DESCRIPTION OF CHARACTER

The pterygoids are parasagittal dentigerous bones located posterior to and often connected with the palatine. The number of teeth (or tooth sockets) on the pterygoid bones was counted. Each bone was recorded separately.

TABLE 158. Frequency distribution of species in range classes of number of pterygoid teeth in families of advanced snakes.

| Classes | Range | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 0 – 6.49 | 12/6 | 8/5 | | | 2/1 |
| 2 | 6.50–13.49 | 48/25 | 9/8 | 8/2 | 11/1 | 27/3 |
| 3 | 13.50–20.49 | 72/36 | 24/15 | 24/10 | 14/5 | 16/2 |
| 4 | 20.50–27.49 | 75/36 | 8/7 | 9/4 | 6/2 | |
| 5 | 27.50–34.49 | 14/10 | 6/3 | | 2/0 | |
| 6 | 34.50–41.49 | 4/1 | 1/0 | | | |
| Totals | | 225/114 | 56/38 | 41/16 | 33/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 159. Spans in number of pterygoid teeth by species and families.

| | | Number of Species | | | | |
|---|---|---|---|---|---|---|
| Span | All families | Colubridae | Elapidae[1] | Hydrophiidae | Viperinae[2] | Crotalinae |
| 1 | 105 | 67 | 14 | 7 | 4 | 13 |
| 2 | 105 | 51 | 21 | 9 | 5 | 19 |
| 3 | 66 | 33 | 5 | 9 | 8 | 11 |
| 4 | 32 | 20 | 3 | 5 | 3 | 1 |
| 5 | 32 | 18 | 5 | 4 | 5 | |
| 6 | 22 | 12 | 3 | 2 | 5 | |
| 7 | 14 | 8 | 2 | 2 | 1 | 1 |
| 8 | 9 | 6 | 1 | 2 | | |
| 9 | 6 | 5 | 1 | | | |
| 10 | 7 | 3 | 1 | 1 | 2 | |
| 11 | 2 | 2 | | | | |
| Totals | 400 | 225 | 56 | 41 | 33 | 45 |
| Span 6 or less | 90.5% | 89.3% | 91.1% | 87.8% | 90.9% | 97.8% |

[1] Including part of Bogert, 1943, Table 2.

[2] Excluding *Azemiops* and *Atractaspis*.

Three states are recognized:

State I —Class 1 (0–6.49)
State II —Classes 2–4 (6.5–27.49)
State III—Classes 5–6 (27.5–41.5)

### Classes and States

The total range of variation in number of pterygoid teeth is segmented by steps of six, since a span of six covers most of the intraspecific variation encountered (90.5 per cent—table 159). Six classes resulted as shown in Table 158. The mean of each taxon was assigned to a class (table 158).

### Familial Ranges of Variation (Table 160)

Colubridae—This family has all three states in a sample of 779 pterygoid bones from 421 skulls of 225 species of 114 genera. State I occurs in 12 species and 6 genera, II in 195 species and 97 genera, III in 18 species and 1 genus.

The range in the number of pterygoid teeth is from 0 (*Aparallactus werneri, Dasypeltis scabra, Lytorhynchus paradoxus*) to 38 (*Mehelya poensis*). The maximum span in a single species is 11 (*Carphophis amoena, Natrix sipedon*). However 89.3 per cent of the species

TABLE 160. Distribution of character states of the number of pterygoid teeth.

| | STATES | | |
|---|---|---|---|
| | I | II | III |
| Classes[1] | 1 | 2–4 | 5–6 |
| | | SPECIES | |
| Colubridae —225 | 5.3% | 86.7% | 8.0% |
| Elapidae — 56 | 14.3 | 73.2 | 12.5 |
| Hydrophiidae— 41 | | 100.0 | |
| Viperinae — 33 | | 93.9 | 6.1 |
| Crotalinae — 45 | 4.4 | 95.6 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 3 | 100.0 | | |
| | | GENERA | |
| Colubridae —114 | 5.3 | 85.1 | 9.6 |
| Elapidae — 38 | 13.2 | 78.9 | 7.9 |
| Hydrophiidae— 16 | | 100.0 | |
| Viperinae — 8 | | 100.0 | |
| Crotalinae — 6 | 16.7 | 83.3 | |
| *Azemiops* — 1 | | 100.0 | |
| *Atractaspis* — 1 | 100.0 | | |

[1] See Table 158.

have a span of six or less (table 159). The maximum span in a single specimen is seven (*Haldea striatula, Ptyas mucosus*).

Elapidae—This family has all three states in a sample of 189 pterygoid bones from 100 skulls of 56 species of 38 genera. State I occurs in 8 species and 5 genera, II in 41 species and 30 genera, III in 7 species and 3 genera.

The range in the number of maxillary teeth is from 0 (*Maticora bivirgata*) to 41 (*Pseudohaje goldii* [Bogert, 1943, Table 2]). The maximum span in a single species is 10 (*Notechis scutatus*). However 91.1 per cent of the species have a span of 6 or less (table 159). The maximum span in a single specimen is 6 (*Dendroaspis angusticeps*).

Hydrophiidae—The sea snakes all have State II in a sample of 239 pterygoid bones from 124 skulls of 41 species of the 16 genera.

The range in the number of pterygoid teeth is from 7 (*Microcephalophis cantoris*) to 28 (*Pelamis platurus*). The maximum span in a single species is 10 (*Hydrophis ornatus*). However 87.8 per cent of the species have a span of 6 or less (table 159). The maximum span in a single specimen is 5 (*Lapemis hardwickii*).

Viperinae—The true vipers have States II and III in a sample of 194 pterygoid bones from 101 skulls of 33 species of the 8 genera. State II occurs in 31 species and 8 genera, III in 2 species.

The range in the number of pterygoid teeth is from 10 (*Bitis arietans, Vipera ammodytes*) to 32 (*Causus lichtensteini*). The maximum span in a single species is 10 (*Causus defilippii, C. rhombeatus*). However, 90.9 per cent of the species have a span of 6 or less (table 159). The maximum span in a single specimen is 6 (*Atheris hindii*).

Crotalinae—The pit vipers have States I and II in a sample of 152 pterygoid bones from 78 skulls of 45 species of the 6 genera. State II occurs in 43 species and 5 genera, I in the 2 species of *Sistrurus*.

The range in the number of pterygoid teeth is from 5 (*Sistrurus catenatus*) to 18 (*Agkistrodon nepa, Bothrops jararacussu, B. schlegeli*). The maximum span in a single species is 7 (*Trimeresurus stejnegeri*). However 97.8 per cent of the species have a span of 6 or less (table 159). The maximum span in a single specimen is 4 (*Bothrops nummifer*).

*Azemiops* has State II in a sample of 4 pterygoid bones from 2 skulls. The range in number of pterygoid teeth is 11 to 14 with a maximum span in a single specimen of 2.

*Atractaspis* has State I in a sample of 8 pterygoid bones from 4 skulls of 3 species. All specimens have no pterygoid teeth.

### PHYLETICS OF CHARACTER 49

Character States I and III are rare in the colubrids (table 160) (Criterion 2).

State I, a small number of pterygoid teeth, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Aparallactus lunulatus*
  - *werneri*
- *Atractus erythromelas*
- *Calamelaps unicolor*
- *Chilorhinophis carpenteri*
- *Dasypeltis scabra*
- *Lytorhynchus diadema*
  - *maynardi*
- *Phyllorhynchus decurtatus*

Elapidae
- *Elaps lacteus*
- *Leptomicrurus collaris*
  - *narducci*
- *Maticora bivirgata*
- *Micrurus fulvius*
  - sp.
  - *spixi*
- *Vermicella annulata*

Crotalinae
- *Sistrurus catenatus*
  - *miliarius*

*Atractaspis bibroni*
- *dahomeyenis*
- *irregularis*

In these colubrids this character state has a higher frequency of correlation with derived states of 17 other characters compared to the frequency distribution of these states of the same 17 characters in the total sample (table 161) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the fossorial habitat (88.9 per cent) compared to the relative abundance of fossorial colubrid species in the total sample (12.4 per cent—table 162) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State I is derived (Criterion 8).

State III, a large number of pterygoid teeth, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
- *Aspidura trachyprocta*
- *Chironius carinatus*
  - *fuscus*
- *Drymobius bifossatus*
- *Hapsidophrys lineata*
- *Liopholidophus lateralis*
- *Meheiya chanleri*
  - *poensis*
- *Natrix erythrogaster*
  - *trianguligera*
- *Oxyrhabdium modestum*
- *Psammodynastes pulverulentus*
- *Rhamnophis aethiopissa*
- *Stegonotus borneensis*
- *Thamnophis marcianus*
  - *sauritus*
- *Tretanorhinus mocquardi*

*Tropidoclonium lineatum*
Elapidae
*Aspidomorphus lineaticollis muelleri*
*Demansia olivacea*
*Hoplocephalus bitorquatus*
*Pseudechis prophyriacus*
*Pseudohaje goldii*
Viperinae
*Causus lichtensteini lineatus*

In these colubrids this character state has a higher frequency of correlation with derived states of nine other characters compared to the frequency distribution of these states of the same nine characters in the total sample (table 161) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the aquatic habitat (33.3 per cent) compared to the relative abundance of aquatic colubrid species in the total sample (14.9 per cent—table 162) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

State I probably arose in a different sequential direction from State III for they correlate mostly with derived states of different

TABLE 161. Correlation of States I and III of Character 49 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State I of Character 49 | In species having State III of Character 49 | In total working sample |
| 2 | 44.4% (3)* | | 15.6% (31) |
| 7 | 66.7 (5) | | 25.5 (56) |
| 13 | 55.6 (4) | | 31.8 (54) |
| 17 | | 72.2% (9) | 35.4 (48) |
| 19 | 88.9 (7) | 52.9 (7) | 36.8 (68) |
| 21 | | 33.3 (5) | 18.9 (29) |
| 22 | 44.4 (4) | 22.2 (11) | 4.5 (11) |
| 28 | 44.4 (3) | | 11.7 (26) |
| 29 | 66.7 (5) | | 10.1 (27) |
| 31 | 37.5 (3) | | 19.5 (44) |
| 32 | 85.7 (5) | | 26.3 (55) |
| 33 | | 61.1 (9) | 43.0 (76) |
| 34 | 62.5 (5) | | 6.8 (18) |
| 37 | 44.4 (3) | 38.9 (6) | 22.9 (54) |
| 39 | 37.5 (2) | | 9.0 (15) |
| 42 | 55.6 (4) | | 8.7 (14) |
| 44 | 50.0 (4) | 37.5 (5) | 5.8 (11) |
| 46 | 44.4 (3) | | 26.9 (52) |
| 47 | | 76.5 (11) | 48.5 (84) |
| 48 | 33.3 (2) | | 6.2 (11) |
| 50 | 62.5 (5) | 61.1 (8) | 20.0 (24) |

* Number of genera.

TABLE 163. Spans in number of dentary teeth by species and families.

| Span | All families | Number of Species |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Colubridae | Elapidae[1] | Hydrophiidae | Viperinae[2] | Crotalinae |
| 1 | 138 | 78 | 22 | 14 | 8 | 16 |
| 2 | 109 | 66 | 17 | 9 | 3 | 14 |
| 3 | 66 | 34 | 5 | 11 | 6 | 10 |
| 4 | 25 | 11 | 4 | 4 | 4 | 2 |
| 5 | 26 | 12 | 3 | 2 | 6 | 3 |
| 6 | 18 | 11 | 2 | 1 | 4 |  |
| 7 | 4 | 4 |  |  |  |  |
| 8 | 3 | 1 | 1 |  | 1 |  |
| 9 | 5 | 4 | 1 |  |  |  |
| 10 | 4 | 4 |  |  |  |  |
| 11 | 2 | 1 |  |  | 1 |  |
| 15 | 1 | 1 |  |  |  |  |
| Totals | 401 | 227 | 55 | 41 | 33 | 45 |
| Span 5 or less | 90.8% | 88.5% | 92.7% | 97.6% | 81.8% | 100.0% |

[1] Including part of Bogert, 1943, table 2.

[2] Excluding *Azemiops* and *Atractaspis*.

TABLE 164. Frequency distribution of species in range classes of number of dentary teeth in families of advanced snakes.

| Classes | Range | Number of species/genera | | | | |
|---|---|---|---|---|---|---|
| | | Colubridae | Elapidae | Hydrophiidae | Viperinae[1] | Crotalinae |
| 1 | 0 – 4.49 | 1/1 | 1/1 | 2/1 | | |
| 2 | 4.50– 9.49 | 11/6 | 3/3 | | | 7/1 |
| 3 | 9.50–14.49 | 30/18 | 20/12 | 14/3 | 5/0 | 23/4 |
| 4 | 14.50–19.49 | 75/40 | 18/14 | 15/8 | 21/7 | 15/1 |
| 5 | 19.50–24.49 | 57/31 | 8/6 | 9/4 | 5/1 | |
| 6 | 24.50–29.49 | 38/11 | 3/1 | 1/0 | 2/0 | |
| 7 | 29.50–34.49 | 12/6 | 1/1 | | | |
| 8 | 34.50–39.49 | 2/1 | 1/0 | | | |
| 9 | 39.50–44.49 | 1/0 | | | | |
| Totals | | 227/114 | 55/38 | 41/16 | 33/8 | 45/6 |

[1] Excluding *Azemiops* and *Atractaspis*.

TABLE 165. Distribution of character states of the number of dentary teeth.

| Classes[1] | | STATES I<br>1–2 | II<br>3–6 | III<br>7–9 |
|---|---|---|---|---|
| | | | SPECIES | |
| Colubridae | —227 | 5.3% | 88.1% | 6.6% |
| Elapidae | — 55 | 7.3 | 89.1 | 3.6 |
| Hydrophiidae | — 41 | 4.9 | 95.1 | |
| Viperinae | — 33 | | 100.0 | |
| Crotalinae | — 45 | 15.6 | 84.4 | |
| *Azemiops* | — 1 | | 100.0 | |
| *Atractaspis* | — 5 | 100.0 | | |
| | | | GENERA | |
| Colubridae | —114 | 6.1 | 87.7 | 6.1 |
| Elapidae | — 38 | 10.5 | 86.8 | 2.6 |
| Hydrophiidae | — 16 | 6.3 | 93.8 | |
| Viperinae | — 8 | | 100.0 | |
| Crotalinae | — 6 | 16.7 | 83.3 | |
| *Azemiops* | — 1 | | 100.0 | |
| *Atractaspis* | — 1 | 100.0 | | |

[1] See Table 164.

State I occurs in 2 species of *Emydocephalus,* II in 39 species of 15 genera.

The range in the number of dentary teeth is from 0 (*Emydocephalus annulatus, E. ijimae*) to 25 (*Aipysurus eydouxi, Hydrophis caerulescens*). The maximum span in a single species is 6 (*Hydrophis brookii*). However, 97.6 per cent of the species have a span of 5 or less. The maximum span in a single specimen is 4 (*Enhydrina schistosa*—MCZ unnumbered).

Viperinae—All taxa of the true vipers have State II in a sample of 181 dentary bones from 101 skulls of 33 species of the 8 genera.

The range in the number of dentary teeth is from 11 (*Vipera russeli*) to 29 (*Causus lichtensteini*). The maximum span in a single species is 11 (*Atheris superciliaris*). However, 81.8 per cent of the species have a span of 5 or less (table 163). The maximum span in a single specimen is 5 (*Causus defilippii*).

Crotalinae—The pit-vipers have States I and II in a sample of 154 dentary bones from 79 skulls of 45 species of the 6 genera. State I occurs in 7 species and 1 genus, II in 38 species and 5 genera.

The range in the number of dentary teeth is from 7 (*Crotalus atrox, C. molossus* ) to 20 (*Agkistrodon nepa*). The maximum span in a single species is 5 (*Agkistrodon contortrix, Crotalus atrox, Tri-*

*meresurus stejnegeri*). The maximum span in a single specimen is 4 (*Bothrops barnetti*—FMNH 9788; *Trimeresurus stejnegeri*—FMNH 127229).

*Azemiops* has State II in a sample of 4 dentary bones from 2 skulls. The range in number of dentary teeth is 15 to 16 with a maximum span of 2.

*Atractaspis* has State I in a sample of 11 dentary bones from 7 skulls of 5 species. The range in the number of dentary teeth is 2 (4 species) to 4 (*A. microlepidota*). The maximum span in a single species is 3 (*A. microlepidota*). The maximum span in a single specimen is 2 (2 species).

### PHYLETICS OF CHARACTER 50

Character States I and III are rare in colubrids (table 165) (Criterion 2).

State I, a small number of dentary teeth, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Atractus erythromelas*
    - *latifrons*
  - *Calamaria leucogaster*
    - *linnaei*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Dasypeltis scabra*
  - *Geophis semidoliatus*
  - *Phyllorhynchus decurtatus*
- Elapidae
  - *Elaps lacteus*
  - *Micruroides euryxanthus*
  - *Parapistocalamus hedigeri*
  - *Vermicella annulata*
- Hydrophiidae
  - *Emydocephalus annulatus*
    - *ijimae*
- Crotalinae
  - *Crotalus adamanteus*
    - *cerastes*
    - *lepidus*
    - *mitchellii*
    - *molossus*
    - *pusillus*
    - *viridis*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of 18 other characters compared to the frequency distribution of these states of the same 18 characters in the total working sample (table 166) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the fossorial habitat (90.9 per cent) compared to the relative abundance of fossorial colubrid species in the total working sample (12.4 per cent—table 167) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State I is derived (Criterion 8).

TABLE 165. Distribution of character states of the number of dentary teeth.

|  |  | STATES |  |
|---|---|---|---|
|  | I | II | III |
| Classes[1] | 1–2 | 3–6 | 7–9 |
|  |  | SPECIES |  |
| Colubridae —227 | 5.3% | 88.1% | 6.6% |
| Elapidae — 55 | 7.3 | 89.1 | 3.6 |
| Hydrophiidae— 41 | 4.9 | 95.1 |  |
| Viperinae — 33 |  | 100.0 |  |
| Crotalinae — 45 | 15.6 | 84.4 |  |
| *Azemiops* — 1 |  | 100.0 |  |
| *Atractaspis* — 5 | 100.0 |  |  |
|  |  | GENERA |  |
| Colubridae —114 | 6.1 | 87.7 | 6.1 |
| Elapidae — 38 | 10.5 | 86.8 | 2.6 |
| Hydrophiidae— 16 | 6.3 | 93.8 |  |
| Viperinae — 8 |  | 100.0 |  |
| Crotalinae — 6 | 16.7 | 83.3 |  |
| *Azemiops* — 1 |  | 100.0 |  |
| *Atractaspis* — 1 | 100.0 |  |  |

[1] See Table 164.

State I occurs in 2 species of *Emydocephalus,* II in 39 species of 15 genera.

The range in the number of dentary teeth is from 0 (*Emydocephalus annulatus, E. ijimae*) to 25 (*Aipysurus eydouxi, Hydrophis caerulescens*). The maximum span in a single species is 6 (*Hydrophis brookii*). However, 97.6 per cent of the species have a span of 5 or less. The maximum span in a single specimen is 4 (*Enhydrina schistosa*—MCZ unnumbered).

Viperinae—All taxa of the true vipers have State II in a sample of 181 dentary bones from 101 skulls of 33 species of the 8 genera.

The range in the number of dentary teeth is from 11 (*Vipera russeli*) to 29 (*Causus lichtensteini*). The maximum span in a single species is 11 (*Atheris superciliaris*). However, 81.8 per cent of the species have a span of 5 or less (table 163). The maximum span in a single specimen is 5 (*Causus defilippii*).

Crotalinae—The pit-vipers have States I and II in a sample of 154 dentary bones from 79 skulls of 45 species of the 6 genera. State I occurs in 7 species and 1 genus, II in 38 species and 5 genera.

The range in the number of dentary teeth is from 7 (*Crotalus atrox, C. molossus* ) to 20 (*Agkistrodon nepa*). The maximum span in a single species is 5 (*Agkistrodon contortrix, Crotalus atrox, Tri-*

*meresurus stejnegeri*). The maximum span in a single specimen is 4 (*Bothrops barnetti*—FMNH 9788; *Trimeresurus stejnegeri*—FMNH 127229).

*Azemiops* has State II in a sample of 4 dentary bones from 2 skulls. The range in number of dentary teeth is 15 to 16 with a maximum span of 2.

*Atractaspis* has State I in a sample of 11 dentary bones from 7 skulls of 5 species. The range in the number of dentary teeth is 2 (4 species) to 4 (*A. microlepidota*). The maximum span in a single species is 3 (*A. microlepidota*). The maximum span in a single specimen is 2 (2 species).

## PHYLETICS OF CHARACTER 50

Character States I and III are rare in colubrids (table 165) (Criterion 2).

State I, a small number of dentary teeth, occurs in the following colubrids (plus other taxa) in our working sample:

- Colubridae
  - *Atractus erythromelas*
    - *latifrons*
  - *Calamaria leucogaster*
    - *linnaei*
    - *schlegeli*
    - *septentrionalis*
  - *Calamelaps unicolor*
  - *Chilorhinophis carpenteri*
  - *Dasypeltis scabra*
  - *Geophis semidoliatus*
  - *Phyllorhynchus decurtatus*
- Elapidae
  - *Elaps lacteus*
  - *Micruroides euryxanthus*
  - *Parapistocalamus hedigeri*
  - *Vermicella annulata*
- Hydrophiidae
  - *Emydocephalus annulatus*
    - *ijimae*
- Crotalinae
  - *Crotalus adamanteus*
    - *cerastes*
    - *lepidus*
    - *mitchellii*
    - *molossus*
    - *pusillus*
    - *viridis*
- *Atractaspis*

In these colubrids this character state has a higher frequency of correlation with derived states of 18 other characters compared to the frequency distribution of these states of the same 18 characters in the total working sample (table 166) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the fossorial habitat (90.9 per cent) compared to the relative abundance of fossorial colubrid species in the total working sample (12.4 per cent—table 167) (Criterion 5).

The application of three criteria (2, 3, 5) suggests that State I is derived (Criterion 8).

TABLE 166. Correlation of States I and III of Character 50 with derived states of certain other characters in Colubridae.

| Character | Frequency of derived states in indicated characters | | |
|---|---|---|---|
| | In species having State I of Character 50 | In species having State III of Character 50 | In total working sample |
| 1 | 45.5% (2)* | | 14.3% (28) |
| 7 | 90.9 (6) | | 25.5 (56) |
| 9 | 54.5 (3) | | 6.8 (14) |
| 11 | 45.5 (2) | 40.0% (4) | 26.7 (50) |
| 13 | 63.6 (5) | | 31.8 (54) |
| 16 | 45.5 (2) | | 21.7 (34) |
| 17 | | 66.7 (4) | 35.4 (48) |
| 19 | 90.9 (6) | | 36.8 (68) |
| 22 | 72.7 (6) | | 4.5 (11) |
| 28 | 60.0 (3) | | 11.7 (26) |
| 29 | 44.4 (4) | | 10.1 (27) |
| 32 | 75.0 (5) | | 26.3 (55) |
| 34 | 55.6 (4) | | 6.8 (18) |
| 38 | 66.7 (4) | | 16.2 (27) |
| 40 | 54.5 (5) | | 24.8 (54) |
| 41 | | 21.4 (3) | 10.9 (20) |
| 42 | 57.1 (4) | | 8.7 (14) |
| 44 | 33.3 (3) | 60.0 (7) | 5.8 (11) |
| 47 | 72.7 (4) | 66.7 (7) | 48.5 (84) |
| 49 | 50.0 (5) | 57.1 (6) | 15.5 (26) |

* Number of genera.

State III, a large number of dentary teeth, occurs in the following colubrids (plus other taxa) in our working sample:

Colubridae
  *Chironius carinatus*
    *fuscus*
  *Dromicodryas bernieri*
  *Liopeltis tricolor*
  *Liopholidophis lateralis*
  *Mehelya poensis*
  *Natrix percarinata*
    *stolata*
    *trianguligera*
    *valida*
  *Oxyrhabdium modestum*
  *Philothalmus irregularis*
  *Thamnophis marcianus*
    *macrostemma*
    *sauritus*
Elapidae
  *Aspidelaps lineaticollis*
    *muelleri*

In these colubrids this character state has a higher frequency of correlation with derived states of six other characters compared to the frequency distribution of these states of the same six characters in the total working sample (table 166) (Criterion 3).

Also these colubrids have a markedly larger number of species confined to the aquatic habitat (46.7 per cent) compared to the rel-

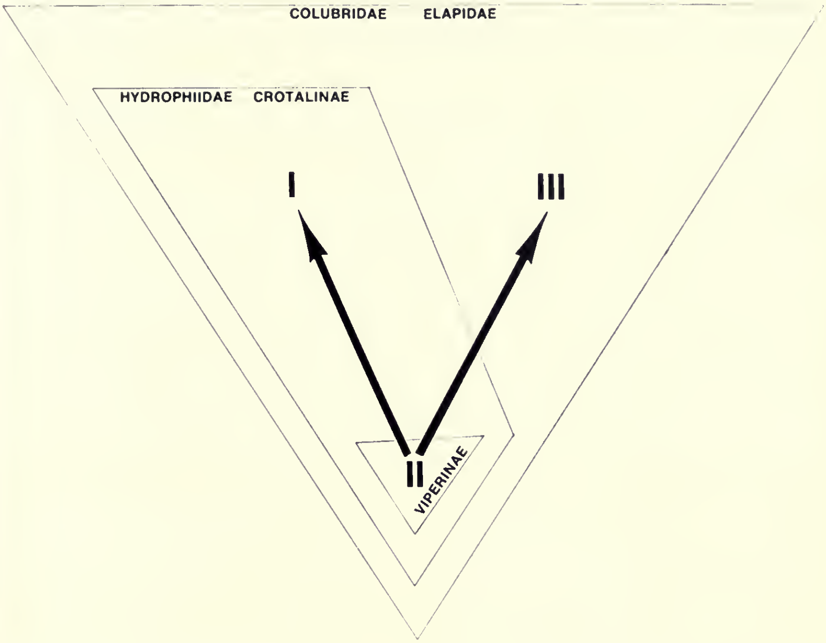

FIG. 52. Distribution among families of states of Character 50. Direction of change among states shown by arrows.

ative abundance of aquatic colubrid species in the total working sample (14.9 per cent—table 167) (Criterion 5).

TABLE 167. Habitat distribution of colubrid species having States I and III of Character 50 compared to the total colubrid working sample.

| | Total Working Sample | State I Character 50 | State III Character 50 |
|---|---|---|---|
| | % | % | % |
| Terrestrial | 36.2 | | 26.7 |
| Arboreal | 16.5 | 9.1 | |
| Aquatic | 14.9 | | 46.7 |
| Subterrestrial | 10.8 | | |
| Fossorial | 12.4 | 90.9 | 6.7 |
| Variation | 5.3 | | 20.0 |
| Unknown | 3.5 | | |

The application of three criteria (2, 3, 5) suggests that State III is derived (Criterion 8).

State I probably arose in a different sequential direction from State III for they correlate mostly with derived states of different characters (table 166) and are predominantly abundant among taxa of different habitat zones (table 167).

The serial nature of this character (i.e., numerical order—table 164, column 2) makes the phyletic arrangement given of the three designated states most probable.

Our interpretation of the phyletics of Character 50 is shown in Figure 52.

## WORKING SAMPLE

The taxonomic working sample is the group of species represented by skull material. This sample was used in our survey of skull characters (Marx and Rabb, 1970, p. 532 and Table III). Emphasis was placed on getting representation of as many genera as possible. The sample has been increased to 510 species compared to the 504 mentioned in Marx and Rabb, 1970, Table III. Skulls are not always complete so that all 50 characters may not be present on the skull(s) of each species. Generic synonyms are given in the index.

COLUBRIDAE
- *Abastor erythrogrammus*
- *Achalinus spinalis*
- *Alsophis dorsalis*
  - *portoreicensis*
  - *sanctae-crucis*
- *Amastridium veliferum*
- *Aparallactus lunulatus*
  - *werneri*
- *Apostolepis ambinigra*
- *Arizona elegans*
- *Arrhyton taeniatum*
  - *vittatum*
- *Aspidura trachyprocta*
- *Atractus elaps*
  - *erythromelas*
  - *latifrons*
  - *ventrimaculatus*
- *Boaedon lineatus*
- *Boiga blandingi*
  - *cynodon*
  - *dendrophila*
  - *irregularis*
  - *jaspidea*
  - *kraepelini*
  - *multimaculata*
  - *pulverulentus*
  - *trigonatus*
- *Bothrophthalmus lineatus*
- *Brachyorrhus albus*
- *Calamaria leucogaster*
  - *linnaei*
  - *pavimentata*
  - *schlegeli*
  - *septentrionalis*
- *Calamelaps unicolor*
- *Carphophis amoena*
- *Cemophora coccinea*
- *Chilomeniscus cinctus*
  - *fasciatus*
- *Chilorhinophis carpenteri*
- *Chionactis occipitalis*
- *Chironius carinatus*
  - *fuscus*
- *Chrysopelea ornata*
- *Clelia clelia*
  - *fitzingeri*
  - *petola*
- *Coluber constrictor*
  - *florulentus*
  - *gemonensis*
  - *hippocrepis*
  - *jugularis*
  - *najadum*
  - *rhodorhachis*
  - *rogersi*
  - *spinalis*
  - *ventromaculatus*
- *Coniophanes fissidens*
- *Conophis lineatus*
- *Conopsis lineatus*
  - *nasus*
- *Coronella austriaca*
- *Crotaphopeltis hotamboeia*

*Cryophis hallbergi*
*Cyclagras gigas*
*Cyclocorus lineatus*
*Darlingtonia haetiana*
*Dasypeltis fasciatus*
  *inornatus*
  *scabra*
*Diadophis amabilis*
  *punctatus*
  *regalis*
*Dimades plicatilis*
*Dinodon rufozonatum*
*Dipsadoboa unicolor*
*Dispholidus typus*
*Drepanoides eatonii*
*Dromicodryas bernieri*
*Dromicus chamissonis*
*Dromophis lineatus*
  *praeornata*
*Dryadophis amarali*
  *boddaerti*
*Drymarchon corais*
*Drymobius bifossatus*
  *margaritiferus*
*Dryocalamus davisoni*
*Duberria lutrix*
*Dugandia bicincta*
*Elachistodon westermanni*
*Elaphe carinata*
  *dione*
  *flavirufa*
  *frenatus*
  *guttata*
  *mandarina*
  *obsoleta*
  *porphyracea*
  *radiata*
  *rufodorsata*
  *schrencki*
  *subocularis*
  *taeniura*
  *vulpina*
*Elapomorphus blumii*
*Enhydris bocourti*
  *chinensis*
  *enhydris*
  *plumbea*
*Erythrolamprus aesculapii*
*Farancia abacura*
*Ficimia publia*
*Gastropyxis smaragdina*
*Geophis multitorques*
  *semidoliatus*
*Gonyosoma oxycephalum*
*Grayia smithi*
*Haldea striatula*
  *valeriae*
*Hapsidophrys lineata*
*Helicops angulatus*
  *carinicauda*
  *leopardinus*
  *schistosus*
*Heterodon nasicus*
  *platyrhinos*
  *simus*
*Holarchus albocinctus*
  *cyclurus*
  *formosanus*
  *hainonensis*
  *violaceus*
*Holuropholis olivaceus*
*Homalopsis buccata*
*Hydraethiops melanogaster*
*Hydrodynastes gigas*
*Hydrops triangularis*
*Hypsiglena torquata*
*Hypsirhynchus ferox*
*Ialtris dorsalis*
*Imantodes cenchoa*
*Lampropeltis elapsoides* (=*t. doliata*)
  *getulus*
  *triangulus*
*Lamprophis aurora*
*Leimadophis melanotus*
  *reginae*
*Leptodeira annulata*
  *maculata*
  *septentrionalis*
*Leptophis mexicanus*
  *occidentalis*
*Limnophis bicolor*
*Liodytes alleni*
*Lioheterodon madagascariensis*
*Liopeltis tricolor*
*Liophis anomala*
  *cobella*
  *miliaris*
*Liopholidophis lateralis*
*Lycodon aulicus*
  *striatus*

*Lycodonomorphus bicolor*
*Lycophidion capense*
*Lygophis boursieri*
  *flavifrenatus*
  *lineatus*
*Lystrophis d'orbignyi*
  *semicinctus*
*Lytorhynchus diadema*
  *maynardi*
*Macrocalamus lateralis*
*Macropisthodon rudis*
*Malpolon moilensis*
  *monspessulanus*
*Manolepis putmani*
*Masticophis flagellum*
  *schotti* (=*M. taeniatus schotti*)
*Mehelya capensis*
  *chanleri*
  *poensis*
*Mimophis mahfalensis*
*Miodon gabonensis*
*Natriciteres olivacea*
*Natrix aequifasciata*
  *annularis*
  *ancscopus*
  *craspedogaster*
  *cyclopion*
  *erythrogaster*
  *kirtlandi*
  *natrix*
  *percarinata*
  *piscator*
  *rhombifera*
  *rigida*
  *septemvittata*
  *sipedon*
  *stolata*
  *taxispilota*
  *tessellata*
  *tigrina*
  *trianguligera*
  *valida*
*Ninia atrata*
  *sebae*
*Oligodon octolineata*
*Opheodrys aestivus*
  *major*
  *vernalis*
*Opisthoplus degener*
*Opisthotropis kuatunensis*
  *latouchi*
*Oxybelis aeneus*
  *argenteus*
  *brevirostris*
  *fulgidus*
*Oxyrhabdium modestum*
*Oxyrhopus petola*
*Passerita mycterizans*
  *nasuta*
  *prasinus*
*Philodryas schotti* (=*Leimadophis poecilogyrus schotti*)
*Philothalmus heterodermus*
  *irregularis*
*Phyllorhynchus decurtatus*
*Pituophis deppei*
  *melanoleucus*
  *sayi*
*Prosymna ambigua*
*Psammodynastes pictus*
  *pulverulentus*
*Psammophis sibilans*
  *subtaeniatus*
*Psammophylax rhombeatus*
*Pseudaspis cana*
*Pseudoboa claelia*
  *clathrata*
  *haasi*
  *neuwiedii*
*Pseudorabdion collaris*
  *longiceps*
*Pseudotomodon trigonatus*
*Pseudoxenodon sinensis*
  *striaticaudatus*
*Pseustes poecilonotus*
  *sulphureus*
*Ptyas korros*
  *mucosus*
*Pythonodipsas carinata*
*Rhacidelus brazili*
*Rhadinaea brevirostris*
  *decorata*
  *serperaster*
*Rhamnophis aethiopissa*
*Rhamphiophis oxyrhynchus*
*Rhinobothryum bovalli*
*Rhinocheilus lecontei*
*Rhinostoma guianense*
*Rhynchocalamus melanocephalus*

- *Salvadora bairdi*
  - *grahami*
  - *hexalepis*
  - *lemniscata*
  - *lineata*
  - *mexicana*
- *Scaphiodontophis annulatus*
- *Scaphiophis albopunctatus*
- *Sibon sibon*
- *Sibynomorphus turgidus*
- *Simophis rhinostoma*
- *Siphlophis cervinus*
- *Sonora episcopa*
  - *semiannulata*
- *Spalerosophis diadema*
- *Spilotes pullulatus*
- *Stegonotus borneensis*
  - *magnus*
- *Stenorhina degenhardti*
- *Stilostoma extenuatum*
- *Storeria dekayi*
  - *occipitomaculata*
- *Tachymenis chilensis*
  - *peruviana*
- *Tantilla gracilis*
- *Telescopus iberus*
  - *semiannulatus*
- *Thamnophis butleri*
  - *eques*
  - *macrostemma*
  - *marcianus*
  - *radix*
  - *sauritus*
  - *sirtalis*
- *Thelotornis kirtlandii*
- *Thrasops flavigularis*
- *Tomodon dorsatus*
  - *ocellatus*
- *Tretanorhinus mocquardi*
  - *variabilis*
- *Trimorphodon lambda*
- *Tripanurgos compressus*
- *Trirhinopholis styani*
- *Tropidocloniom lineatum*
- *Tropidodipsas fischeri*
  - *philippi*
- *Uromacer catesbyi*
  - *oxyrhynchus*
- *Xenodon colubrinus*
  - *merremii*
  - *severus*
- *Zaocys dhumnades*
  - *nigromarginatus*

ELAPIDAE

- *Acanthophis antarcticus*
- *Apistocalamus lonnbergi*
  - *loriae*
- *Aspidelaps lubricus*
  - *scutatus*
- *Aspidomorphus lineaticollis*
  - *muelleri*
- *Boulengerina annulata*
- *Brachyaspis curta*
- *Brachyurophis semifasciata*
- *Bungarus candidus*
  - *fasciatus*
  - *multicinctus*
- *Cacophis harriettae*
- *Calliophis japonicus*
- *Demansia olivacea*
  - *textilis*
- *Dendroaspis angusticeps*
  - *jamesoni*
  - *polylepis*
  - *viridis*
- *Denisonia coronoides*
  - *fasciata*
  - *nigrescens*
  - *par*
  - *superba*
  - *woodfordi*
- *Elapognathus minor*
- *Elaps lacteus*
- *Elapsoidea sundevalli*
- *Furina diadema*
- *Glyphodon tristis*
- *Hemachatus haemachatus*
- *Hoplocephalus bitorquatus*
  - *bungaroides*
- *Leptomicrurus collaris*
  - *narducci*
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- *Micropechis elapsoides*
  - *ikaheka*
- *Micruroides euryxanthus*
- *Micrurus affinis*
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  - *lemniscatus*
  - *mipartitus*

- *nigrocinctus*
- sp.
- *spixi*

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- *fuscus*
- *laevis*

*Astrotia stokesii*
*Emydocephalus annulatus*
- *ijimae*

*Enhydrina schistosa*
*Ephalophis greyi*
*Hydrelaps darwiniensis*
*Hydrophis belcheri*
- *brookii*
- *caerulescens*
- *cyanocinctus*
- *fasciatus*
- *inornatus*
- *kingi*
- *klossi*
- *lapemoides*
- *major*
- *mamillaris*
- *melanocephalus*
- *melanosoma*
- *mertoni*
- *ornatus*
- *torquatus*

*Kerilia jerdoni*
*Kolpophis annandalei*
*Lapemis curtus*
- *hardwickii*

*Laticauda colubrina*
- *laticaudata*
- *schistorhynchus*
- *semifasciata*

*Microcephalophis cantoris*
- *gracilis*

*Pelamis platurus*
*Thalassophina viperina*
*Thalassophis anomalus*

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- *worthingtoni*

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- *berus*
- *latasti*
- *lebetina*

- *persica*
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AZEMIOPINAE
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CROTALINAE
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  - *contortrix*
  - *halys*
  - *hypnale*
  - *nepa*
  - *piscivorus*
  - *rhodostoma*
  - *strauchi*
- *Bothrops alternatus*
  - *atrox*
  - *barnetti*
  - *cotiara*
  - *dunni*
  - *godmanni*
  - *jararacussu*
  - *lansbergii*
  - *neuwiedi*
  - *nummifer*
  - *schlegeli*
- *Crotalus adamanteus*
  - *atrox*
  - *basiliscus*
  - *cerastes*
  - *durissus*
  - *horridus*
  - *lepidus*
  - *mitchellii*
  - *molossus*
  - *pusillus*
  - *ruber*
  - *viridis*
- *Lachesis mutus*
- *Sistrurus catenatus*
  - *miliarius*
- *Trimeresurus albolabris*
  - *flavoviridis*
  - *jerdoni*
  - *monticola*
  - *mucrosquamatus*
  - *okinavensis*
  - *puniceus*
  - *stejnegeri*
  - *sumatranus*
  - *wagleri*

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- *dahomeyensis*
- *irregularis*
- *microlepidota*

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